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STUDIES ON THE GROWTH OF GORILLA AND OF OTHER HIGHER  
PRIMATES WITH SPECIAL REFERENCE TO A FETUS OF  
GORILLA, PRESERVED IN THE CARNEGIE MUSEUM

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(Plates I-VIII and Six Text-figures)

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(EIGHT PLATES AND SIX TEXT-FIGURES.)

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## PART I.

## Chapter 1. INTRODUCTION.

The inseparable problems of human evolution and of man's exact place among the primates can be expected to be solved only by a consideration of the findings from *all* the many different fields of science which have evidence to offer for the reconstruction of the pedigree of the primates. The contributions from the various sciences to our knowledge of the higher primates still differ markedly in amount and significance. The prenatal development of the apes ranks probably first among the phases of which least is known to-day. Indeed, much less information is available as to embryos and fetuses of the anthropoids than in regard to fossil apes. Few fetuses of apes have been collected and some of these have either never been described at all, or are merely mentioned in a few words.<sup>1</sup> Still other fetuses have been erroneously identified. Breschet (1845)\* was the first author to deal with what he supposed to be the fetus of a higher ape; he labelled this specimen "*Semnopithecus Hilobates*. Gibbon?". The writer is firmly convinced that this fetus is not that of a gibbon, but one of some short-tailed macaque.<sup>2</sup> On the other hand, the fetus pictured by Darwin (1874) is a gibbon fetus and not that of an orang, as Darwin states, nor that of a chimpanzee, as Schmidt (1892)

\* The dates in brackets refer to the Bibliography, which is appended.

<sup>1</sup> For instance, Lönnberg (1917) lists a chimpanzee fetus in a report on mammals collected in Central Africa; and Prince William of Sweden (1923) mentions that a gorilla fetus was obtained on his expedition, but, as far as the writer is aware, no description of these valuable specimens has appeared as yet. Huxley (1864) devoted only a few words to a chimpanzee fetus; and Anthony (1918), in his detailed description of the brain of a gorilla fetus and of a chimpanzee fetus, gives merely a photograph and a few measurements of the entire specimens.

<sup>2</sup> The upper extremity of this specimen is much too short for a gibbon fetus and the tail would no longer be visible in a gibbon at this stage of development (See Chapter 8, coccygeal tubercle). Several other points support the author's diagnosis: such as the formation of the forehead, of the outer ear, of the foot, and of the placenta.

tried to prove later on.<sup>3</sup> The first thorough description of an anthropoid fetus (orang-utan) is given in the excellent paper by Trinchese (1870). This was followed by Deniker's (1885) classic monograph on a gorilla fetus. To these have since been added a few more or less extensive reports on other ape fetuses; most noteworthy among which are the papers by Schwalbe (1911) and by Bolk (1926 b). The rapid and fundamental changes occurring during intra-uterine life necessitate the study of a great many specimens at different stages of development in order to gain even the barest outlines of prenatal growth. Information on the embryonic period in apes is practically restricted to the one gibbon and one orang embryo described by Keibel (1906). In writing a review of the fetal growth of primates the author (1926 b) collected the few scattered data from the literature and combined these with his own observations in order to give at least a preliminary sketch of some of the fetal conditions in apes.

There can be no doubt that investigations on the ontogeny of the higher primates will be of most essential help in the solution of the problems of primate phylogeny in general and of human evolution in particular, but many more reports on additional material are needed.

In the present paper it is intended first of all to contribute some observations on a new fetus of one of the apes. The author is indebted for this opportunity to Dr. W. J. Holland, who has generously entrusted him with the description of the fetus of a gorilla (Plate I). Since there exist publications on several other gorilla fetuses it seems desirable to discuss them all together and to add to this study of fetal life such data on postnatal growth in the gorilla as are available in the literature and are made possible through an examination of material in various collections. In this attempt to establish the more important changes, which take place during growth in one of the anthropoid apes, it became necessary for a correct interpretation of the findings to compare the conditions in gorilla with those in other representatives of the higher primates. However, these comparisons could not be made as extensive, as might seem desirable, on account of the scarcity of corresponding data on other apes, which will first have to be augmented and subjected to separate study.

<sup>3</sup> Deniker had suspected that this specimen might be a gibbon fetus and not an orang-utan fetus, but Schmidt objected to the "gibbon" determination chiefly on the ground that the ischial callosities were missing. The writer has studied a considerable number of gibbon fetuses and is thus in a position to state that these callosities appear very late in the gibbon (See Chapter 8). The illustration and measurements by Schmidt of the specimen in question agree so closely with the author's data on gibbon fetuses that there can be no doubt of its being a gibbon. Schwalbe was evidently misled by the form of the ear, (which, as Schmidt showed, is due to artificial deformation) in stating that the gibbon fetus, pictured by Darwin, was in his opinion the fetus of a macaque (G. Schwalbe in "Evolution in Modern Thought," Modern Library, New York, p. 119).



The entire investigation is restricted to the characters observable on the outer body and will deal particularly with the body proportions, which are of such outstanding interest in studies of growth. Most of the literature appertaining to growth in gorilla deals with the outer body and its proportions. Of the fetuses of gorilla, for instance, only the specimen of Deniker was actually dissected. The fetus, described for the first time in this paper, belonging to the Carnegie Museum has not been dissected. It was hoped at first that the skeletal system of this specimen could be studied by means of X-ray photographs, but since it had been preserved in formalin for the past sixteen years no satisfactory results could be obtained in that way.<sup>4</sup>

## Chapter 2. MATERIAL.

As mentioned above, a special effort was made in this study to collect from the widely scattered literature those data which have a bearing upon the problem of growth in gorilla. It will be helpful to other students to enumerate here these sources of information and to establish also the age sequence of all the available material. This sequence is chiefly based upon the size of the specimens. Since frequently no measurement of total size has been recorded, the length of the limbs has to serve in such instances as the only possible criterion for the relative age of the specimen.

I.<sup>5</sup> The youngest gorilla fetus on record is the specimen described by Duckworth (1904 a). This fetus is male, and belongs to one of the subspecies of *Gorilla gorilla*. The distance from vertex to coccyx (straight) amounts to 71 mm., the length of the upper arm is 21 mm., and the combined length of thigh and leg equals 30 mm. In its state of development this specimen corresponds most closely to human fetuses of the twelfth or thirteenth week (menstrual age).

II. The gorilla fetus described for the first time in this paper is considerably older than Duckworth's specimen. This fetus is female and corresponds in development to human fetuses of the beginning of the fifteenth week. The distance from vertex to coccyx measures 85 mm., the sitting height is 88.5 mm., the length of the upper arm is 25 mm., and the total length of thigh and leg amounts to 40 mm.

<sup>4</sup> The writer wishes to express his sincere thanks to Dr. E. C. Hill for his persistent and most skilful efforts to obtain good X-ray photographs of this fetus.

The placenta, uterus, and ovaries, which Dr. Holland kindly sent with the gorilla fetus, have been studied by the author's colleagues, Dr. G. B. Wislocki and Dr. C. Hartman, who will report elsewhere on this rare material. (A discussion of this gorilla placenta will appear in a paper by Wislocki, 1927, which is now in press).

<sup>5</sup> Wherever a particular specimen is referred to hereafter these numbers of age sequence will be given. All the specific names in this paper are according to Elliot (1913).

All these surpass the corresponding dimensions of fetus I. This fetus belongs to the Carnegie Museum (Acc. No. 7698) and was collected by the medical missionary, Dr. Hymen L. Weber, in the vicinity of Efulen, Cameroon, in 1910. Dr. Holland has kindly informed the author that this specimen belongs either to *Gorilla gorilla diehli* or to *Gorilla gorilla matschiei*, but that it is assigned with greater probability to the former subspecies.

III. According to its size the gorilla fetus of Deniker (1885) ranks third, corresponding in development to human fetuses of the eighteenth or nineteenth week. This fetus is female, was obtained in West Africa, and hence belongs in all probability to the species *Gorilla gorilla*. The distance from vertex to coccyx measures 135 mm., the upper arm has a length of 53 mm., and the total length of thigh and leg amounts to 82 mm.

IV. The fourth gorilla fetus is that described recently by Bolk (1926 b). Since this author does not state in which part of Africa his specimen was obtained but mentions that it was brought to Amsterdam a long time ago, it can be assumed that it belongs most likely to the *Gorilla gorilla* group and not to the much rarer and more recently discovered East African *Gorilla beringei*. This fetus is male and corresponds in size to human fetuses of the beginning of the sixth month, but in regard to certain other characters of development it seems better comparable to human fetuses of the middle, if not end, of the sixth month. The straight distance from the vertex to the anus amounts in this gorilla fetus to 170 mm., the upper arm is 54 mm. long, and femur and tibia combined have a length of 92 mm.

V. The fifth gorilla fetus is in all probability of the same stage of development as Bolk's specimen; it may be even slightly younger. Unfortunately, Anthony (1918), who described the brain of this fetus, gives only a photograph of the entire specimen (Photograph reproduced on Pl. II, fig. 1) and one of a plaster cast thereof. This fetus is male, came from the French Congo, and belongs, therefore, to one of the subspecies of *Gorilla gorilla*. The distance from the vertex to the coccyx (taken with a tape) is given as approximately 190 mm.; it is to be regretted that no other measurements have been published.

No information of any sort is available in regard to the last part of fetal growth in gorilla.

VI. The next stage in the development of gorilla is represented by the interesting photographs of a gorilla baby published by Reichenow (1921). These pictures were taken at intervals from the age of one month to that of seven months. Reichenow's paper contains no measurements. This specimen was obtained in Cameroon and belongs to the species *Gorilla gorilla*.



VII. The youngest gorilla infant, of which there exist measurements, is the specimen described by Ehlers (1881). It is a male, undoubtedly of the *Gorilla gorilla* group, according to Ehlers less than one year of age, and measures from vertex to coccyx 308 mm. The upper arm length is 114 mm. and the length of thigh and leg amounts to 172 mm.

VIII. Next in age is the female infant (*G. gorilla*) measured by Mollison (1911). From the height of the trunk (208 mm.) and the various indices given by Mollison the upper arm length of this specimen is calculated as 146 mm. and the thigh-plus-leg length as 231 mm. These values are very considerably above the corresponding measurements of Ehlers' infant, thus indicating a marked difference in age between specimens VII and VIII.

IX. The infant described by Deniker (1885) is but little older, *i.e.*, larger, than the infant just mentioned. This specimen is a female with a distance between vertex and coccyx of 405 mm., an upper arm length of 165 mm., and a thigh-plus-leg length of 259 mm. That it must be of the species *Gorilla gorilla* is evident from the fact that the Mountain Gorilla was still unknown at the time of Deniker's publication.

X. Famelart (1883) has published some few measurements on a male gorilla infant, which he kept alive for a few months. According to this author it was captured when about seven months old and had then a sitting height of 320 mm. which is about the same as in infant VII with its distance from vertex to coccyx (somewhat less than sitting height!) of 308 mm. The head measurements were taken by Famelart about three months later, when the animal had attained a size slightly above that of infant IX, judging by its sitting height which had increased to 410 mm. or more (?). This specimen is assigned to the species *Gorilla mayema* Alix and Bouvier, or, as called by Elliot (1913), *Pseudogorilla mayema*.

XI. Information on this stage of growth is available in regard to the proportions of the limbs. These proportions were obtained from measurements on three infantile skeletons of *Gorilla gorilla*. Data for one of these were published by Deniker (1885) and for another by Bolk (1926 b). A third specimen was kindly measured for the author by Dr. W. L. Straus, Jr. in the collection of the Department of Anatomy of Western Reserve University. The lengths of the humeri of these infants average 168 mm. A detailed enumeration of the limb proportions of all the gorilla skeletons, used for this paper, will be found in Table 5. In the tables on growth only the average proportions of these skeletons will be quoted.

XII. The last specimen which could properly be called an infant is the second gorilla (*G. gorilla*) measured by Mollison (1911). From the trunk height

and the proportions of this young female the length of the upper arm is calculated as 212 mm. and the thigh-plus-leg length as 322 mm.

XIII. The juvenile male *Gorilla gorilla*, measured by Bolau (1876), must be considerably older than gorilla XII, since its thigh-plus-leg length amounts to 385 mm. The only other measurement, given by Bolau, which may be used for a determination of relative age, is the combined length of upper arm and forearm amounting to 430 mm. This dimension is calculated as 386 mm. for gorilla XII and amounts to 445 mm. in the next specimen.

XIV. The second juvenile is a male *Gorilla beringei* which the author has studied at the American Museum of Natural History. This specimen was unfortunately skinned and eviscerated so that some measurements could not be taken at all and for the others certain corrections had to be made to allow for the thickness of the skin. These corrections were based upon comparisons between the author's measurements on a chimpanzee of similar age before and after it was skinned. The sitting height of this gorilla amounts to 619 mm., the distance from vertex to coccyx to 587 mm., the upper arm length equals 254 mm., and the thigh-plus-leg length 387 mm.

XV. The average limb proportions of three juvenile skeletons of *Gorilla gorilla* represent the next stage. Data on one of these skeletons were given by Mollison (1911) and on another by Bolk (1926 b). The third skeleton belongs to the collection of the Laboratory of Physical Anthropology, Johns Hopkins University. The average length of the humerus of this series, which is 261 mm., stands between the length of the upper arm of gorilla XIV (254 mm.) and that of gorilla XVI (275 mm.).

XVI. Sommer (1907) has published some measurements on an adult female gorilla ("*Gorilla castaneiceps* Slack" = *G. gorilla castaneiceps*). However, this specimen, which had lived in captivity for seven years, is probably not of normal size for its age, since its sitting height, for instance, measures only 610 mm. The upper arm length of 275 mm. is very little above the humerus length of the juvenile skeletons. The thigh-plus-leg length equals 475 mm. The last two dimensions fall below the range of variation of these measurements in other adult female gorillas (XVII and part of series XVIII). Further remarks on the size of this specimen will be found in Chapter 5. Good photographs of this animal, when alive, have been published by Grabowsky (1906).

XVII. The female *Gorilla gorilla*, described by Ehlers (1881), is the only adult gorilla of typical size in the flesh of which detailed and reliable measurements have been published as far as the author could ascertain. This specimen



had a complete second dentition and all the epiphyseal lines of the long bones were obliterated. The distance between vertex and coccyx is given as 700 mm., the upper arm length as 339 mm., and the thigh-plus-leg length as 535 mm.

XVIII. In order to place at least some of the proportions in adult gorilla on a more representative basis than is afforded by the above specimens alone, the average limb proportions of 38 adult skeletons of West African gorillas (*G. gorilla* and its various subspecies?) have been figured from data in the literature and from measurements of specimens in various collections. Publications of the following authors were consulted in assembling this series: Du Chaillu (1861) one skeleton; Deniker (1885) one skeleton; Mollison (1911) sixteen skeletons; Lorenz v. Liburnau (1917) three skeletons; and Bolk (1926 b) two skeletons. In addition measurements by Dr. W. L. Straus, Jr. on five skeletons in the collection of the Western Reserve University were incorporated and also the results of the author's examination of nine skeletons in the collections of the U. S. National Museum, the American Museum of Natural History, the Department of Zoology of Columbia University, and the Anthropological Laboratory of Johns Hopkins University, as well as of one skeleton from West Africa, measured some time ago in a dealer's store in Berlin.

In order to test the question whether there are any specific differences between the proportions of *Gorilla gorilla* and *Gorilla beringei*, five adult skeletons of the latter type were measured by the author and their limb proportions compared with those of the above series XVIII. Four of these rare skeletons of the Mountain Gorilla are from the American Museum of Natural History and one from the National Museum. For the purpose of certain further comparisons use was made of measurements by Lorenz v. Liburnau (1917) on the limb bones of five adult Mountain Gorillas of the species *Gorilla graueri* Matschie.

Two stages of the growth of gorilla were selected for detailed comparison with representatives of the other higher primates at corresponding ages. The first stage is given by the fetus (II) of the Carnegie Museum, the only specimen of prenatal growth of which a complete set of measurements is available. The second stage was chosen to represent the completion of growth, *i.e.*, adult life. The special technique employed for these comparisons required observations on a considerable number of individuals of at least one of the higher primates in order to establish some measure for range of variation. A larger series of cases of the same age is available for man only. The following material, or papers describing certain material, was assembled for these comparisons:

*For the stage of fetal growth:*

1. Twenty human fetuses (white) from the end of the fourteenth and the beginning of the fifteenth week, ranging in sitting height from 85 to 92 mm., with an average sitting height of 88.5 mm., *i.e.*, exactly the same as in gorilla fetus II.

2. The youngest chimpanzee fetus on record is that described by Friedenthal (1914). This specimen is somewhat larger than gorilla fetus II, but is the only one which can serve for comparison. The distance from the vertex to the symphysis pubis is obtained as 99 mm. by adding certain measurements given by Friedenthal. This dimension corresponds to a sitting height of approximately 110 mm. Judging by the photograph of this specimen, its stage of development can not differ very markedly from that of gorilla fetus II.

3. Of the four orang-utan fetuses, of which measurements have been published by Schwalbe (1911), specimen No. 3 agrees in its size most closely with gorilla II. The vertex-coccyx length, taken with a tape, amounts in both to 115 mm., the greatest head length is in the orang 35 mm. and in the gorilla 34.1 mm. It can be assumed that the sitting height (straight measurement) of this orang fetus must be also very similar to that of the gorilla fetus, *i.e.*, approximately 88.5 mm.

4. A gibbon fetus (*Hylobates concolor*) of a stage of development corresponding to that of gorilla II was measured by the author. This specimen belongs to the collection of the late Prof. E. Selenka (No. 24 a). It has a sitting height of 56 mm.

*For the stage of adult growth:*

5. Twenty-four adult white men from eighteen to twenty-five years of age. These adults, as well as the above mentioned human fetuses (Series 1), had been measured by the author in connection with his extensive investigations on human growth. Full details on these series will be published in a later paper.

6. Measurements on a fully adult chimpanzee have been published by Friedenthal (1914). This specimen is a female, weighing 55 kgm.

7. An adult orang-utan in a perfect state of preservation was measured by the author at the American Museum of Natural History (Department of Comparative Anatomy, No. 563). This ape is a female and has a sitting height of 717 mm.

8. The adult gibbon used in this paper was also measured by the author. This specimen is of the same species (*Hylobates concolor*) as fetus 4 and belongs also to the Selenka collection (No. 16 a). It has a sitting height of 237 mm.

The author wishes to take this opportunity to express his sincere thanks to Mrs. E. Selenka, Prof. W. K. Gregory, Prof. J. H. McGregor, and Mr. G. S. Miller, Jr., for their ready and generous permission to study the valuable material mentioned above. The writer is furthermore indebted to his former student, Dr. W. L. Straus, Jr., who kindly measured for him the gorilla skeletons in the collection of Western Reserve University, and to Prof. T. W. Todd, who very obligingly permitted this.

## Chapter 3. TECHNIQUE.

The measurements taken on this primate material correspond, wherever possible, to those generally used in anthropometry (See Martin, 1914). Many measurements have to be taken in order to express accurately the dimensions



and proportions of every part of the body. It is very essential that such measurements are defined precisely, so that the recorded data are not open to misinterpretation. Unfortunately it is often very difficult, and sometimes impossible, to make use of some measurements given in the literature, simply because authors have omitted to state their methods of measuring.

The following list of measurements explains the technique adopted by the author. The diagram on Pl. III, fig. 1 obviates a detailed description of many dimensions. The specimen, no matter of what age, is first placed flat on its back with its spine practically straight and its head posed so that an imaginary plane, determined by the ear openings and the lowest point of one orbit (ear-eye horizon), stands perpendicular to the body axis. All the "height" measurements on the trunk and the head are taken strictly parallel to the body axis, as represented by the table on which the specimen rests.

*General measurements:*<sup>6</sup>

1. Sitting height: from vertex to buttocks over ischial tuberosities (See Pl. III, fig. 1).
2. Stature: can be taken directly only in man after birth. In all primate fetuses and in all apes the knees are flexed so that the approximate stature is best obtained by the addition of measurements 3, 16, and 17.
3. Cephalo-thoraco-abdominal height: vertex to upper edge of symphysis pubis (symphysis).

*Trunk measurements:*

4. Anterior trunk height: suprasternal notch to symphysis.
5. Acromion height: middle of line connecting the lateral points on acromial processes of shoulder blades (acromion) to symphysis.
6. Shoulder height: projective height of acromion over suprasternal notch (obtained by subtraction of m. 4 from m. 5).
7. Nipple height: middle of line connecting centers of nipples to symphysis.
8. Umbilicus height: center of attachment of umbilical cord or center of umbilical scar to symphysis. This measurement can not be taken in many adult apes, since they frequently have no trace of an umbilical scar left.
9. Shoulder breadth: distance between right and left acromion.
10. Hip breadth: distance between most lateral points over the great trochanters.
11. Nipple breadth: distance between centers of nipples.
12. Transverse chest diameter: at level of sternal attachment of fourth pair of ribs.
13. Sagittal chest diameter: at same level as m. 12.
14. Chest circumference: at same level as m. 12 and m. 13.

*Limb measurements:*

15. Total lower limb length: obtained by addition of m. 16 and m. 17.
16. Thigh length: length of femur taken laterally from top of great trochanter.
17. Knee—sole length: length of tibia plus foot height, taken medially.
18. Leg length: length of tibia to tip of internal malleolus.

<sup>6</sup> Wherever the absolute measurements are referred to hereafter their serial number will be given together with the letter *m* to distinguish them from the relative measurements, or indices, the numbers of which will be accompanied by an *i*.

19. Foot length: from heel to tip of longest toe.
20. Great toe length: from heel to tip of hallux (hallux adduced).
21. Foot breadth: greatest width between metatarso-phalangeal joints of toes II to V.
22. Total upper limb length: obtained by addition of m. 23, m. 24, and m. 25.
23. Upper arm length: length of humerus from acromion to humero-radial joint.
24. Forearm length: length of radius to tip of styloid process.
25. Hand length: from middle of line connecting tips of ulnar and radial styloid processes to tip of middle finger.
26. Thumb length: from styloid process of radius to tip of thumb (thumb adduced).
27. Hand breadth: greatest width between metacarpo-phalangeal joints of fingers II to V.

*Head measurements:*

28. Average head diameter (head module): sum of m. 30, m. 32, and m. 33 divided by 3.
29. Average head circumference: arithmetic mean of the three circumferences in the three different dimensions, *i.e.*, sum of m. 34, (m. 35 + m. 31), and (m. 36 + m. 37) divided by 3.
30. Head length: greatest length of brain part of head (from glabella).
31. Nasion—inion length (base length): point overlying middle of naso-frontal suture (nasion) to occipital protuberance (inion), measured in a straight line.
32. Head breadth: greatest breadth of brain part of head between parietals or temporals.
33. Head height: upper end of tragus (tragion point) to vertex, projective height perpendicular to ear—eye horizon.
34. Horizontal head circumference: at level of m. 30.
35. Sagittal arc of head: distance between the two end points of m. 31, taken with tape.
36. Transverse arc of head: distance between the two tragion points, taken with tape over vertex.
37. Biauricular breadth (base breadth): distance between the end points of m. 36, taken in a straight line.
38. Total head height: from chin to vertex.
39. Total face height: from chin to nasion.
40. Upper face height: from middle of mouth to nasion.
41. Face breadth: width between most lateral points over zygomatic arches.
42. Nose height: from nasion to lowest point on nasal septum.
43. Nose breadth: greatest width between nasal wings (in some of the apes impossible to determine exactly).
44. Interocular breadth: distance between inner angles of eye-clefts.
45. Biocular breadth: distance between outer angles of eye-clefts.
46. Mouth breadth: greatest horizontal width of closed mouth, measured in a straight line.
47. Ear height: greatest height of outer ear.
48. Ear breadth: greatest width of outer ear, perpendicular to m. 47.

With these measurements it is possible to construct complete and very accurate diagrams of the body proportions of any specimen, as shown, for instance, on Pl. III, fig 2.

A few additional measurements had to be taken solely in order to render the author's material directly comparable to certain data in the literature. These substituted measurements, which had to be used in some of the tables, are the following:

- 1a. Vertex—coccyx length (somewhat smaller than sitting height).
- 9a. Deltoid breadth: greatest width between deltoid muscles (somewhat larger than shoulder breadth).
- 10a. Pelvic breadth: greatest distance between iliac crests (differs from hip breadth in varying degree).
- 28a. Average head diameter: considering only head length and head breadth, but not head height, as does m. 28.



From these absolute measurements, which are always given in millimeters, a series of proportions or indices is formed, in which the measurements are invariably expressed in percentage of one another. A considerable number of these relative measurements are not ordinarily adopted by the author. Their selection for this study was largely governed by the particular measurements, available in the literature, which often left no choice for other and more significant proportions. Since most authors have recorded but few measurements there will be unfortunately frequent gaps in the tables of indices.

A number of evident errors were detected among the measurements available in the various publications on gorilla and other apes. At times these errors could be corrected,<sup>7</sup> but more often the doubtful data had to be discarded. On the other hand, in some cases it was possible to calculate certain essential measurements from published figures for other dimensions of the same specimen.<sup>8</sup>

#### Chapter 4. GORILLA FETUS II.

All the absolute measurements and a few other data on the gorilla fetus of the Carnegie Museum are recorded in this preliminary chapter. The proportions and many other features of this specimen will be discussed together with all the other material in the later chapters.

Plate I gives two general views of the fetus as it was fixed by preserving fluid in the natural position which it maintained in the uterine cavity. This particular position, which very closely resembles that of the average human

<sup>7</sup> For instance, Friedenthal (1914) gives the thigh length of a chimpanzee fetus (2) as 24.5 mm. and the leg length of the same specimen as 27 mm.; these two figures undoubtedly have been reversed by the printer, since no chimpanzee has a greater length of the tibia than of the femur. In the same way the head length and breadth of Friedenthal's adult chimpanzee (6) should be reversed, since no ape has a head length of 191 mm. combined with a breadth of 257 mm. The gorilla fetus III can not have an anterior trunk height of only 54 mm. and an umbilicus height of 24 mm., as stated by Deniker, but, judging by the excellent photographs in natural size of this specimen, the former measurement must be at least 59 mm. and the latter not more than 12 mm. Deniker's two figures resulted in impossible proportions, but from the latter, carefully corrected figures, indices are obtained, which do not remove this specimen too far from the other gorilla fetuses. Of this same fetus III Deniker has published the measurements of the long bones of the limbs as well as those of upper arm, forearm, etc. Since these two sets of supposedly closely corresponding measurements agree but slightly (*e.g.* leg length = 33 mm., tibia length = 35 mm.; thigh length = 49 mm., femur length = 44 mm.) the writer has used Deniker's skeletal measurements wherever possible.

<sup>8</sup> For instance, among Ehlers' (1881) measurements on two gorillas (VII & XVII) are listed the distances from vertex to suprasternal notch and to symphysis, by subtraction of the former from the latter distance the anterior trunk-height is obtained. By similar methods it was possible to calculate from available figures certain additional measurements for the specimens of Ehlers, Sommer, and Mollison.

fetus seems to be maintained by gorilla with little variation throughout at least the middle of its fetal life. The text-figures given by Deniker show that the specimen of that author had its head and limbs flexed in a very similar manner. The older gorilla fetuses of Bolk and of Anthony (See Plate II, fig. 1) are bent even more than fetus II. It is particularly noteworthy that in all these fetuses the feet are posed so that their soles stand in almost parallel planes, facing one another. In human fetuses of the same growth period the feet have moved much further downward and the tibiæ are rarely directed transverse to the body axis, as in the gorilla fetuses.

The umbilical cord of fetus II, which has a length of 156 mm., is very little twisted and was not wound around the body, as in Bolk's specimen.

Table 1 compares the absolute measurements of gorilla fetus II with the corresponding average dimensions on human fetuses of the same stage of development.

TABLE 1.

Absolute measurements (in mm.) of Gorilla Fetus II and of Human Fetuses (Series I, average) of corresponding development.

No. of Measurements	Gorilla Fetus II.	Human fetuses	No. of Measurements	Gorilla Fetus II.	Human fetuses
1. Sitting height.....	88.5	88.5	25. Hand length.....	20.0	12.0
2. Stature.....	123.3	124.3	26. Thumb length.....	9.6	8.8
3. Cephalo-thoraco-abdom. h.....	79.5	79.6	27. Hand breadth.....	7.8	6.5
4. Anterior trunk height.....	40.6	38.4	28. Average head diameter.....	29.4	29.7
5. Acromion height.....	48.4	41.2	29. Average head circumference....	96.8	101.0
6. Shoulder height.....	7.8	2.8	30. Head length.....	34.1	33.5
7. Nipple height.....	34.0	29.8	31. Nasion—inion length.....	33.0	30.6
8. Umbilicus height.....	8.5	6.6	32. Head breadth.....	31.0	29.3
9. Shoulder breadth.....	29.6	25.6	33. Head height.....	23.2	26.2
10. Hip breadth.....	18.8	18.7	34. Horizontal head circumference..	102.0	101.6
11. Nipple breadth.....	16.9	15.2	35. Sagittal arc of head.....	60.3	72.7
12. Transverse chest diameter.....	29.2	26.2	36. Transverse arc of head.....	65.2	72.6
13. Sagittal chest diameter.....	26.8	21.8	37. Biauricular breadth.....	30.0	25.7
14. Chest circumference.....	94.0	79.0	38. Total head height.....	34.3	35.5
15. Total lower limb length.....	43.8	44.7	39. Total face height.....	16.4	13.7
16. Thigh length.....	22.6	23.4	40. Upper face height.....	12.7	9.1
17. Knee—sole length.....	21.2	21.3	41. Face breadth.....	26.7	24.7
18. Leg length.....	17.8	17.7	42. Nose height.....	9.0	6.2
19. Foot length.....	19.0	14.4	43. Nose breadth.....	12.0	6.3
20. Great toe length.....	16.9	13.8	44. Interocular breadth.....	7.6	8.5
21. Foot breadth.....	6.0	4.4	45. Biocular breadth.....	18.6	18.6
22. Total upper limb length.....	66.3	50.8	46. Mouth breadth.....	12.0	8.6
23. Upper arm length.....	25.0	22.2	47. Ear height.....	9.0	7.1
24. Forearm length.....	21.3	16.7	48. Ear breadth.....	6.1	4.2

The chief results from this comparison are illustrated on Pl. III, fig. 2. It is first of all apparent that the gorilla, though of identical sitting height and almost the same stature as the average of the human fetuses, is much more bulky than the latter. This is best shown by the difference in body weight, that of the



gorilla being 64.2 gm. whereas the average weight of the human fetuses is only 50.6 gm. That the chest in the gorilla fetus is proportionately wider than in the human fetus is evident from a comparison between the shoulder breadth, chest circumference, and chest diameters of the two (See Table 1). The gorilla fetus, when contrasted with human fetuses, is furthermore characterized by long upper limbs, long and slender hands and feet, and a large face. The brain part of the head is slightly longer and broader but much lower in the gorilla than in the human fetus. The neck of the former is strikingly thick and short, a condition which appears emphasized through the extremely high location of the shoulder (See Pl. III, fig. 2). Most of these features represent indications of the much more marked differences which exist between adult gorilla and man.

## PART II.

### Chapter 5. RATE OF GROWTH.

There exist but meagre data bearing upon the duration of the various phases of growth in the higher apes, so that little can be said in regard to the important problems of their rate of growth and the possible fluctuations thereof. Deniker (1885) supposes that the duration of pregnancy in anthropoids varies between eight and nine months. According to v. Allesch (1921) a pregnant chimpanzee menstruated until five months before she gave birth to a baby, but he does not consider this conclusive, since he states: "Man hat also die Wahl, eine Tragzeit von nur 5 Monaten anzunehmen oder mit der Möglichkeit zu rechnen, dass die Blutung auch noch beim tragenden Tier ein oder mehrere Male weiterdauert." There can be no doubt that pregnancy in the large apes extends over a longer period than five months since Cuvier found it to last seven months in such low forms as macaques. Bolk (1926 b) assumes that gestation in gorilla is shorter than in man, since the former weighs at birth considerably less than the latter. However, the size of the fetus at term is among different primates apparently not correlated with the duration of their intra-uterine growth, as is shown by the following facts. Pregnancy in man lasts nine months and the birth weight is about six or seven pounds. In a captive chimpanzee Montané (1916) found the duration of gestation to be also nine months, although the weight of a newborn chimpanzee is only little above two pounds (Blair, 1920). Since the prenatal life of the chimpanzee has been established by Montané as being of the same length as in man, it can hardly be assumed that the gorilla would differ in this respect. Reichenow (1921) captured a gorilla baby (VI), only a few days old, which weighed two

kilograms. Bolk's gorilla fetus weighs exactly one pound and, therefore, must be still far from term.<sup>9</sup>

Body weight varies very considerably at any age in man and, apparently, also in gorilla. For instance, the male gorilla baby (X), captured by Famelart, was in this author's opinion about seven months old, yet it weighed only two kilograms, *i.e.*, as much as Reichenow's new-born. Of course, the above estimate of age may be too high, but the animal must have been at least two months old, since two incisors had erupted in the upper jaw and four in the lower jaw. Akeley (1923) gives the following interesting quotation from a letter by an English hunter: ". . . shot a female [Mountain Gorilla] with a young one in her arms . . . The baby was apparently not more than 24 hours old . . . The baby gorilla (a female) is now two months old and in the best of health and weighs nine pounds. She has cut six teeth. She does not show any signs of walking yet . . .".<sup>10</sup> Considering the reports by the last two authors, it seems most probable that the average weight of the gorilla at birth is even somewhat less than that of Reichenow's new-born, and certainly less than the average weight in man at birth, but more than that of the chimpanzee. Since the periods in which these birth weights are acquired are in all likelihood the same for man and the higher apes, it may be concluded that the average rate of prenatal growth is less in the gorilla and the chimpanzee than in man.

During early infancy the chimpanzee continues to lag behind man in its weight. According to Yerkes (1925) a chimpanzee, born in Cuba, weighed at the age of two years only twelve pounds, and it is stated to be a "remarkably healthy, well-nourished, and altogether normal individual." During later infancy and childhood some chimpanzees grow more rapidly as shown by the following figures, mentioned by Heck (1916): One chimpanzee increased in weight during five years from eleven to twenty-three kilograms, another one grew in the same interval from seven and one-half to twenty-five kilograms, and a third animal multiplied

<sup>9</sup> The gorilla fetus V is at practically the same stage of development as Bolk's specimen (IV); both correspond to human fetuses of the sixth month. Anthony (1912) has published two photographs of the mother animal of fetus V, taken immediately after her death. Judging by these illustrations, which show a tremendously enlarged abdomen, even this relatively early stage of pregnancy is most conspicuous in the gorilla. It is easily as noticeable as in man and apparently more so than in the chimpanzee, since v. Allesch (1921) reports that the appearance of a pregnant chimpanzee in the Berlin Zoological Garden did in no respect begin to change until two months before the birth of her young. Even during this last period, when her abdomen became enlarged, it never protruded beyond the chest and, incidentally, her breasts remained unaltered in size.

<sup>10</sup> The captive gorilla baby of Reichenow (1921) made the first attempts at walking at the age of seven and a half months, as shown by interesting photographs in this author's publication.



its initial weight even almost four times in four years, namely from fifteen to fifty-eight kilograms—an astoundingly rapid gain.

No gorilla has ever been born in captivity, so that the determinations of age for this ape are always rather roughly estimated. The author had an opportunity to examine the young male West African gorilla "John Daniel II" in May 1924. At that time this ape was said to be about four to four and a half years old; it had an approximate standing height of 106 cm. and weighed about eighty pounds. Yerkes (1927) mentions that the female Mountain Gorilla "Congo", studied by him, had an approximate age of four to five years, weighed about sixty-five pounds, and had a standing height of 96.5 cm. ( $\pm 2.5$  cm.). These data indicate that gorillas must grow rather rapidly, at least during the later part of infancy. This is also borne out by the following records: Famelart's male gorilla baby (X) measured 32 cm. from vertex to anus at the time it was captured, when it was said to be about seven months old. After only two months this dimension had increased to 41 cm. A young male gorilla, kept alive for two years by Falkenstein, increased in weight during that time from fourteen to twenty-one kilograms (quoted by Heck, 1916). According to Hornaday (1922) the young gorilla "John" (= "John Daniel I"?), when purchased in London, weighed thirty-two pounds. Two years and three months later it had reached the weight of one hundred and twelve pounds, *i.e.*, three and a half times the initial weight. A very much slower increase occurred in the female gorilla (XVI), which lived for over seven years in the Zoological Garden of Breslau. This animal had, when received, an estimated age of about four years, and weighed thirty-one and one half pounds. During the first four years of captivity it grew in weight only to sixty pounds (Grabowsky, 1906), which is very little even for a female and arouses the suspicion that the animal (though stated to be perfectly healthy) may have been kept on an insufficient diet, or without adequate exercise or sunlight.

The duration of the total postnatal growth period in the higher apes is known with certainty only in the case of the chimpanzee. Sir Edwin Ray Lankester (1915) states that the female chimpanzee "Sally" at the London Zoological Garden was full-grown and adult at the age of eight years. The mother of the first chimpanzee born in New York (*Pan chimpanse*) was ten years old and the father (*Pan schweinfurthi*) had an approximate age of eight years (Blair, 1920). Mitchell (1912) is of the opinion that the period of growth in anthropoid apes lasts eight to twelve years. The above mentioned female gorilla from Breslau showed undoubted signs of sexual maturity at the age of five years, and grew very little (only six pounds) from the age of eight years to her death at eleven years, so that she was quite

mature and full-grown at eight years, provided that the estimate of four years as the age of her capture is correct.

A few figures will suffice to give an approximate idea of the weight of the body in adult apes. According to Bauman (1926) the full-grown female chimpanzee "Suzette" of the New York Zoological Park weighed one hundred and thirty-five pounds and her male companion, "Boma," had a weight of one hundred and sixty-five pounds. The large female chimpanzee "Johanna" of the Zoological Garden in Philadelphia weighed at the time of her death one hundred and sixty pounds. The writer has been assured by experienced and reliable dealers in animals that some male chimpanzees may attain a much greater weight than the figures above quoted.

It is well known that adult gorillas are very much heavier than adult chimpanzees. Akeley (1923) gives the weight of an adult male as three hundred and sixty pounds, and Prince William of Sweden (1923) quotes three hundred and thirty pounds for a full-grown male gorilla. Even much higher figures are found in the literature, but these are mostly estimates, and not actual weights, as in the above two cases. For instance, Heck (1916) mentions a giant gorilla, which was killed by H. Paschen in 1900 in Cameroon. This specimen, which is now in the Tring Museum, is reported to have a standing height of over two meters and a "conservatively estimated" weight of two hundred and fifty kilograms!

From these notes it may be concluded that at the completion of growth the chimpanzee is nearly or quite as heavy as man and that the gorilla greatly surpasses man in bulk. Since the final weight in apes is attained in considerably less time than in man (in only eight or ten years), and, since the weight at birth of the apes (chimpanzee slightly over two pounds, gorilla four pounds) is less than in man, the general intensity and rate of postnatal growth must be much higher in these apes than in man. This rate is particularly striking in the gorilla, which may increase in weight from four pounds or less at birth, to three hundred and sixty pounds and more, in adult life, and this during as short a period as eight to ten years. It is very interesting and significant to find that the gorilla, according to all available data, grows more slowly than man before birth, but much more rapidly than man during postnatal life.

#### Chapter 6. PIGMENTATION.

Gorilla fetus I is entirely unpigmented, since Duckworth states that its skin is uniformly whitish. The only pigmentation of the next oldest specimen, fetus II, occurs on the ears, which are of a light brown color (See Pl. I), in striking contrast



to the rest of the body, which is still absolutely white. It may be mentioned here that Schwalbe (1911) found in a somewhat older fetus of orang-utan the ears, the nasal bridge, and some parts in the pelvic region a much darker brown than the remaining surface of the body. It seems, therefore, that pigmentation in the anthropoids begins in localized zones, similar to the condition in the negro, in whom the first pigment appears on the scrotum. Deniker's gorilla fetus (III) is of a light brown color, except the face, palm, and sole, which are more of a yellowish tone; the darkest pigmentation is found on the back. It is interesting that fetus IV, which is considerably older than Deniker's specimen, is according to Bolk less pigmented than the younger fetus. This fact indicates a variability in the age of beginning pigmentation in gorilla similar to that observed by the author in negro fetuses, in which, however, the skin commences to darken at a later stage of development. Bolk states that the color of the skin of his gorilla fetus is not much different from that of a white human fetus, except that one can detect an indication of yellow and on the back a faint brownish tint. Reichenow's gorilla baby showed at the approximate age of one month a still fairly light chocolate-brown color (See Pl. II, fig. 3), which, however, darkened very rapidly, having in the third month turned into black. Du Chaillu (1861) states that the color of the skin of young and of adult gorillas is intense black.

In the chimpanzee the pigment of the skin apparently develops sooner than in the gorilla. The chimpanzee fetus (*Pan kooloo-kamba*) of Friedenthal (1914), which has a total weight of only three hundred and seventy grams, already shows a rather dark skin and perfectly black hair (Friedenthal, 1908 a). Bolk's (1926 b) chimpanzee fetus, which weighs six hundred and sixty grams, has a much darker skin than the slightly younger gorilla fetus of the same author. The excellent photograph by Anthony (1918) of an older chimpanzee fetus ("*Anthropopithecus Tschego* Duv." = *Pan satyrus* ?), measuring from vertex to coccyx 250 mm., shows a skin, which seems to be considerably darker than even that of Reichenow's gorilla baby at the age of one month. This last mentioned gorilla appears to be lighter also than the new-born chimpanzee, described by Blair (1920), which, however, was not yet as dark as a chimpanzee baby weighing six and one half pounds, and about a year, or less, old.<sup>11</sup> The author is convinced that at this stage of growth, or sooner, the skin of chimpanzee is in general as dark as it ever becomes, since none of the many older chimpanzees examined by him had developed darker hues. Certain parts of the skin, particularly over the face, ears, chest,

<sup>11</sup> Prof. McGregor kindly permitted the author to examine this specimen. The preserved body of the new-born chimpanzee, mentioned above, was generously lent to the writer by the late Prof. Huntington.

palms, and soles, remain in many species of chimpanzee rather pale throughout life, while other parts may become somewhat darker in their pigmentation but only few species have really very dark skins, comparable to those of gorillas.

These notes, together with the author's observations on the color of the skin in extensive series of negro fetuses and infants, permit the conclusion that pigmentation begins in chimpanzee at an earlier stage of development than in gorilla, the latter being intermediate in this respect between the former and the negro. In all three forms the final and darkest pigmentation is not reached until some time after birth.

Bolk (1917) found deep blue pigmented areas, of a nature identical with the so-called Mongolian spots in man, over the iliac crests of his chimpanzee fetus, which corresponds in development to human fetuses of the sixth, or at most seventh month. The writer has never found any Mongolian spots in human fetuses of that age, but has observed them frequently in white as well as negro fetuses close to term. This difference serves as a further support for the conclusion that pigment develops earlier in the ape than in man. In orang-utan the coloring of the skin appears at least as early as in the chimpanzee and hence also very much sooner than in man. Schwalbe (1911) reports that an orang fetus (No. 3, Chapter 2), which is of the same stage of development as gorilla fetus II, has a brownish color on the entire body.

To these notes on pigmentation must be added the remark of Famelart (1883) that the color of the eye of his infant gorilla changed during one month from yellow to chestnut-brown.<sup>12</sup> Finally, it may be mentioned that the literature contains several reports, which claim that the color of the hair of gorilla changes at least locally during childhood and again during old age. The hair itself develops some time before any pigment appears in it, since all the hairs of gorilla fetus II are absolutely colorless, whereas in fetus III they are pigmented.

#### Chapter 7. HAIR.

The prenatal development of hairs is strikingly similar in anthropoid apes and man. Gorilla fetus I does not as yet show any hair at all. The first hair, which appears in fetus II, must be described in some detail. Faint indications of hair follicles can be detected under a magnifying glass on most parts of the body, but macroscopically visible hair is present only on the eye-brows, lips, and chin, *i.e.*,

<sup>12</sup> Some shade of medium dark brown seems to be the normal color of the iris in juvenile gorillas. It was noted by the author on the young gorillas "John Daniel II" and specimen XIV. Friedenthal (1910), moreover, gives a colored illustration of a young gorilla with a brown iris. The adult gorilla XVI had according to Heine (1906) a dark brown iris. Hartmann (1889), too, mentions that the iris of the gorilla darkens with age.



on the same places as in human fetuses (See Pl. VIII, Fetus II). The slightly more than two hundred hairs of the region of the eyebrows meet in the midsagittal plane, but are much shorter in the glabellar zone than above the eyes. In the middle portion all the hairs point straight upward, but towards the sides they diverge laterally, assuming finally a horizontal direction. The hairs on the upper lip diverge sharply from the center, pointing slightly upward near the mid-line, but changing gradually to a slightly downward direction above the corners of the mouth. All the hair on the lower lip and chin is directed downward. Since none of these hairs exceed 0.33 mm. in length, their direction was determined on enlarged photographs.

In gorilla fetus III the eyelashes have appeared; the hair on the eyebrows has reached a length of 5 to 7 mm.; the hair on the scalp is fairly well developed, though still short; and many parts on the trunk and limbs bear a coat of very short hair. (Many further details are given by Deniker, 1885). Bolk (1919 and 1926 b) has published exhaustive reports on the hair of gorilla fetus IV and on that of a slightly older chimpanzee fetus. One of the most interesting findings on these two specimens is the fact that the hair on their scalp is very much longer than on the rest of the body. In the gorilla it extends down to the eyebrows, whereas in the chimpanzee it leaves the forehead practically bare. In a younger chimpanzee fetus Friedenthal (1908 a) had already found this striking condition, and states that the body was covered with fine and extremely short hair, but that strong black hair of very considerable length extended over exactly the same area of the top of the head as in man. The chimpanzee fetus, pictured by Anthony (1918), shows surprisingly long black hairs on top of the head, but very little hair on the rest of its body. Montané (1916) states that the chimpanzee, born in Cuba, was at birth "completely hairless" with the exception of the head, the scalp bearing abundant hair. The new-born chimpanzee, shown on many illustrations by Blair (1920), likewise has the longest hair on the scalp, but in addition the outside of the limbs and the back already bear hair of considerable length. However, that there are chimpanzees in which the hair of the body in general does not attain any noteworthy length until a considerable time after birth, is proved by the baby from Cameroon, pictured by Matschie (1919). This chimpanzee is practically naked, except for long hair on the crown of its head and the sides of its face. Only its middle incisors have erupted, so that it must have been two months old, since in the above mentioned Cuban chimpanzee these teeth did not appear until two months after its birth. Data for still later growth changes in the hair of chimpanzee (*Pan schweinfurthi*) are given in the following instructive quotation from Allen



(1925): "In the youngest specimen, in which the incisors and canines are only beginning to break through the gums,<sup>13</sup> the whole underside of the body and inside of the limbs is nearly naked and pale yellowish brown like the face. The whole head is heavily clothed with black rather soft hair about 25 mm. long; the rest of the upper parts are thinly haired, the skin showing through; the hair is much shorter and thinner than on the head. At a later stage (milk dentition, m<sup>1</sup> not fully mature) the body is well clothed . . ." Further information on the hair changes in the apes is contained in the following quotation from v. Allesch (1921) appertaining to a chimpanzee, born in the Zoological Garden in Berlin: "Das erste Haar [at birth] war sehr lang, schlicht, völlig schwarz, am Kopf klar gescheitelt. Am Ende der vierten Woche ging es aus. . . Schon in der nächsten Woche kam das neue Haar, das anfangs kürzer blieb und einen leichten Stich ins Bräunliche aufwies."

The gorilla baby VI was, when captured, very sparsely covered with hair, appearing almost naked, but on the crown of its head there arose a tuft of very long brown hair (See Pl. II, fig. 3). Within a few months the body was covered with a dense coat of hair, extending also over the forehead, which at first was entirely bare.

As yet unfinished studies of the author on large series of fetuses, new-borns, and infants of monkeys permit the preliminary and very generalized statement that there exists a greater difference in the conditions of growth of the hair between the monkeys and the anthropoid apes than between the latter and man, except, of course, in late stages of growth.

#### Chapter 8. TRUNK.

All the available data for changes of growth in the proportions of the trunk in the gorilla are listed in Table 2. A glance at this table with its many gaps in the rows of figures makes it at once apparent that as yet but little can be definitely said in regard to the growth of the trunk. The ontogenetic changes in some of the most important proportions of the trunk can not be studied at all, since the necessary measurements were not taken on their material by other authors. There can be no doubt that there exists a very pronounced variability in gorillas, so that part of the irregular age-changes in the indices of Table 2 may be accounted for on that basis. However, it has also to be borne in mind that some of the measurements in the literature, from which indices have been formed, may not have been taken accurately, or at least not in exactly the same way as supposedly

<sup>13</sup> Judging by the teeth, this specimen must be several months old and not, as Allen states, "apparently only a few days old." The lateral incisors in the above mentioned Cuban chimpanzee baby did not erupt until the third month.

corresponding measurements by other authors. Table 2, and the other following tables on growth, do not pretend to show detailed ontogenetic changes based on typical figures, but represents rather a first attempt to gain some preliminary idea of the general trend of certain proportions during advancing age.

TABLE 2.  
Growth Changes in the Proportions of the Trunk of Gorilla.

Index No.	Percentage relation between:	Fetus I	Fetus II	Fetus III	Infant VII	Infant VIII	Infant IX	Infant XII	Juv. XIII	Juv. XIV	Adult XVI	Adult XVII
1.	Chest circumfer. (m.14) & Trunk h. (m.4)	221.2	231.5	281.5	....	....	....	....	....	171.6	180.0	....
1 a.	Chest circumfer. (m.14) & Stature (m.2)	83.0	76.2	84.7	....	....	71.0	....	76.9	62.6	69.9	....
2.	Shoulder br. (m.9) & Trunk h. (m.4)	....	72.9	....	64.1	....	....	70.0	....	61.9	....	60.8
2 a.	Deltoid br. (m.9a) & Trunk h. (m.4)	....	83.3	93.1	121.9	....	....	....	....	....	77.5	....
3 a.	Pelvic br. (m.10a) & Trunk h. (m.4)	....	60.6	54.9	79.7	59.9	62.0	....	71.0	....	54.9	....
4 a.	Pelvic br. (m.10a) & Shoulder br. (m.9)	....	....	75.3	....	103.7	....	....	101.3	....	88.7	....
4 b.	Pelvic br. (m.10a) & Deltoid br. (m.9a)	....	72.7	59.0	65.3	....	....	....	....	....	....	....
7 a.	Nipple br. (m.11) & Trunk h. (m.4)	....	33.3	41.6	54.2	32.3	....	....	36.0	....	....	....
8.	Nipple h. (m.7) & Trunk h. (m.4)	....	....	83.7	....	....	....	....	83.0	....	....	....
9.	Umbilicus h. (m.8) & Trunk h. (m.4)	....	18.2	20.9	20.5	....	....	....	27.0	....	....	15.0
											17.8	

The chest circumference decreases in relation to the trunk height (i 1) as well as in relation to the stature (i 1a) as growth proceeds, a change which agrees very closely with that in most other primates, including man (See Schultz, 1926 b). After the age of twenty years or later the relative chest girth of men shows frequently a tendency toward a late secondary increase. A similar condition seems to exist in male gorillas, since an old male Mountain Gorilla had according to Akeley (1923) a stature of sixty-seven and one half inches and a chest circumference of sixty-two inches. From these dimensions index 1 a is calculated as 91.9 which is far above the value for the adult female gorilla XVI and the juvenile male Mountain Gorilla XIV. Indeed, this widening of the chest, late in life, seems to be much more pronounced in gorilla than in man. The large apes and man have developed a broad and stout trunk of great proportionate bulk, which is far removed from the long and slender trunk of lower primates. Gorilla has reached a greater extreme in this respect than man, a difference which exists already in fetuses (See Chapter 4).

The relative width of the shoulders (i 2 & i 2a) shows in general a tendency to decrease with age. The proportions based upon pelvic breadth vary so markedly that no clear changes of age can be recognized in the few available figures. From a study of photographs and skeletons of adult gorillas the author would expect that the pelvic breadth of adult males is smaller than the shoulder breadth, resulting in a proportion (i 4a) considerably lower than the value of 106.1, found in the adult female. Such a sexual difference in adult gorillas would be analogous to that existing in regard to this proportion between adult man and woman.



The nipples of gorilla are situated near the axillæ but not as much so as, *e.g.*, in the orang-utan; their exact position on the trunk seems to vary, as in other primates, more in a horizontal than in a vertical direction. That the nipples lie higher up on the trunk in gorilla than in man is evident from the following comparison: i 8 amounts to 83 in an infantile gorilla but averages 76 in human infants. In fetal life, however, this distinction is not yet present, since the same index amounts to 83.7 in gorilla fetus II and reaches a maximum in human fetuses of corresponding development of 85.3 (See Table 8).

In all primates the umbilicus shifts to a relatively higher position on the trunk with advancing growth (Schultz, 1926 b). In gorilla this tendency prevails also during fetal and infantile life, but subsequently the index for this relative position (i 9) would undergo a marked drop in case the low values in the two adult gorillas can be relied upon. If any trace at all of an umbilical scar is left in adult apes, this is usually so faint and uncertain that erroneous determinations of its location can easily be made.<sup>14</sup> It seems advisable, therefore, to await further data on the relative position of the umbilicus in adult gorilla and to consider the present evidence as insufficient for concluding definitely that the umbilicus shifts downward late in growth.

The lower end of the trunk of gorilla fetus II shows several features which necessitate detailed discussion. The tip of the tail in this specimen has not yet disappeared, or, more specifically, has not yet become overgrown by neighboring tissue (See Pl. IV, fig. 2). This last remnant of an outer tail is called "coccygeal tubercle", corresponding to its German name "Steisshöcker". This appellation in its strictest sense perhaps may not be entirely justifiable, since the tip of the last coccygeal vertebra reaches only to the base of this tubercle. The form and location of this fetal structure leave no doubt that it corresponds to the end of the relatively much larger embryonic tail and, incidentally, not to the so-called caudal filament, which develops temporarily on the embryonic tail.<sup>15</sup> In man

<sup>14</sup> Ehlers (1881) himself states that he is not quite certain whether he located the umbilicus in his adult gorilla (XVII) correctly. The measurements by the same author on the position of the umbilicus in the gorilla infant VII must contain some very evident error, since, when figured with the writer's method, the height of the umbilicus (m. 8) is found to equal 101 mm., whereas the height of the trunk (m. 4) amounts to 170 mm. These values combine in the impossible proportion (i 9) of 59.4, according to which the umbilicus would have been situated over the lower end of the sternum!

<sup>15</sup> It is most likely this caudal filament, and not the end of the true tail, which has persisted in those rare cases of "external tails" found among man and apes at stages of growth long after that, in which the last trace of a tail has normally disappeared from the surface. For instance, the minute pendulous appendage over the coccyx of a young chimpanzee, which has been pictured by Rosenberg (1876), resembles in every detail an undoubtedly persisting caudal filament, found and studied by the author in a human fetus of the fifth month (No. 730, Carnegie Laboratory of Embryology).



the coccygeal tubercle disappears normally in fetuses ranging in sitting height between 33 and 52 mm. (Kunitomo, 1918). In rare instances it may persist to the 60 mm. stage, but most frequently it is already missing in specimens of 40 mm. It is very surprising to find from the data collected in Table 3 that the stage of development, in which this tubercle disappears, is so greatly at variance in the

TABLE 3.

Fetuses and infants of the higher apes, for which definite information is available in regard to the presence or absence of the coccygeal tubercle. The vertex-coccyx curve is always considerably longer than the corresponding straight measurement on the same specimen. All measurements are given in millimeters.

Primate:	Number	Age	Vertex-coccyx (straight) or Sitting height:	Vertex-coccyx curve (with tape):	Observer:	Coccy- geal tubercle:
GIBBON	I	fetus	21.5	....	Schultz	<i>present</i>
	II	fetuses	56 to 173	....	Schultz	absent
	23	fetuses	....	62 to 222	Schwalbe, 1911	absent
	I	fetus	136	....	Schmidt, 1892	absent
ORANG-UTAN	I	fetus	....	56	Schwalbe, 1911	<i>present</i>
	I	fetus	....	75	Schwalbe, 1911	<i>present</i>
	I	fetus	....	115	Schwalbe, 1911	absent
	I	fetus	approx. 135	177	Schwalbe, 1911	<i>present</i>
	3	fetuses	145 to 230	....	Schultz	absent
	4	infants	264 to 317	....	Schultz	absent
CHIMPANZEE	I	fetus	185	.....	Bolk, 1926 b	<i>present</i>
	I	newborn	260	....	Schultz	absent
	I	infant	337	....	Schultz,	absent
GORILLA	I	fetus	88.5	....	Schultz	<i>present</i>
	I	fetus	135	....	Deniker, 1885	absent
	I	fetus	170	....	Bolk, 1926 b	absent

different apes. In the gibbon the coccygeal tubercle was well developed in a fetus of 21.5 mm. but in two specimens of respectively 56 and 62 mm. sitting height (one measured straight, the other one in a curve) no trace of this structure was remaining, and in 33 older fetuses the tubercle was also missing. In the gibbon, therefore, the tubercle disappears at an early stage of development, just as in man. In gorilla it persists considerably longer, *i.e.*, at least to the 88 mm. stage. In orang-utan it is found in a still larger fetus, though in another one (No. 3, Chapter 2) of the same size as gorilla fetus II it has already disappeared. Chimpanzee retains this structure longer than any of the other higher primates, since it is very conspicuous in a fetus with a sitting height of 185 mm. The author is unable to advance any plausible hypothesis to account for this wide discrepancy in the time of the final ontogenetic disappearance of the tail. One might be inclined at first to explain these embryological findings by the assumption that the phylogenetic degenera-

tion of the tail had occurred earlier in man and gibbon than in the three large apes. Such a possibility, however, is rendered highly improbable by the fact that the reduction of the tail has reached a greater extreme in adult orang-utan than in adult man (Wiedersheim, 1908; Schultz, 1926 a).

The female external genitalia of gorilla fetus II correspond fairly closely to those of a human fetus of the same stage of development (See Pl. IV, fig. 2). The groove on the lower side of the clitoris is very little developed in the gorilla. The labia majora of the latter are relatively smaller than in the human fetus, but they are rather high and hence clearly visible in a side view of this specimen (See Pl. I). Under the magnifying glass hair follicles can be recognized on the labia majora of the gorilla fetus, so there can be no doubt as to their identity. In Deniker's gorilla fetus III the labia majora are proportionately very much larger than in specimen II. They are also very well developed in the still older chimpanzee fetus, described by Bolk (1926 b). During postnatal life the labia majora undergo a marked reduction in the three large apes, indeed, many authors have claimed that they are entirely missing. Thus Bischoff (1879) and Gerhardt (1906) did not find these structures in gorilla, the former having studied three young specimens, the latter an adult. Deniker (1885), on the other hand, reached the conclusion from his material that the labia majora do not disappear completely in gorilla and in orang. Bischoff, likewise, observed a faint indication of these labia in the latter ape and Klaatsch (1892) found them in a juvenile orang. Friedenthal (1910), however, is of the opinion that the labia majora, observed by him in an orang, are not directly comparable to those in women. The same author denies their existence in chimpanzee, as does Bischoff, but a number of other authors, as *e.g.*, Symington (1889), Sperino (1897), and Sonntag (1923), have examined female chimpanzees which possessed rudimentary but undoubted labia majora. The conflicting reports on this point permit the conclusion that the degree of ontogenetic reduction of the labia majora varies a great deal in the anthropoids. It is certain that these structures are laid down in fetal life, but, whereas in man they persist throughout growth, in the anthropoids they undergo a process of atrophy, which in many cases leads sooner or later to their complete disappearance. It is very interesting to find that the gibbons and siamangs stand in this respect closer to man than do the three large apes, since the labia majora in the family *Hylobatidae* are not only well developed in the fetus, but are retained as comparatively large structures throughout postnatal growth, when the labia minora are



becoming smaller and gradually almost or entirely disappear from outside view (See Pl. IV, fig. 3.)<sup>16</sup>

This consideration of the conditions on the lower end of the trunk must include some remarks on the ischial callosities which are usually claimed to be totally absent in the anthropoid apes. Several authors have published independently and without referring to one another various observations which contradict the above mentioned claim. These observations will be quoted in the following and thus be brought together for the first time. Some brief remarks on the ontogenetic development of ischial callosities will be added in the hope that these combined notes may lead to a better understanding of the gradual evolutionary disappearance of these structures among the higher primates.

Friedenthal (1908 b) has given an illustration of well formed ischial callosities in an adult male orang-utan (*l.c.*, fig. 1, plate VIII) and one of small but well defined callosities in a young male chimpanzee (*l.c.*, fig. 7, plate III). In the same publication this author states: "Bei Schimpanse (Gorilla?) und Orang bilden sich im späteren Leben in Anpassung an das Sitzen auf den Sitzknorren schwache Gesässchwielen aus, welche nicht wie beim Menschen durch die starke Gesässmuskulatur vor Druck geschützt werden, wenn auch niemals so auffällige hornige Schwielen gebildet werden wie bei der Mehrzahl der Ostaffen." Lönnberg (1917) observed these callosities in chimpanzee and traces of them in gorilla. Speaking of *Gorilla beringei mikenensis* he says: "There are [in one adult female] no regular or distinct ischiadic callosities, but in the place of such there is a bare patch on either side, and the skin of these is, in counteraction to the rubbing and wearing, thickened and the horny layer has a tendency of peeling off in flakes. It may be said to be ischiadic callosities in being. In the old male there is no trace of such a bare place, but in the semi-adult male the hair is worn off on two symmetrically situated small spots in the ischiadic region corresponding to these patches in the female." Lönnberg's description of a series of ten chimpanzees (*Anthropopithecus cottoni*) from one locality contains the following comment: "All the adult specimens are provided with very well developed ischiadic callosities. These are largest in the old ones, f. i. 7 x 4 cm. in the old male; 6.5 x 3.5 cm. in the oldest female. The callosities are so thoroughly developed that they can be seen very plainly from the inner side of the skin as well. In the young animal with milk-dentition the

<sup>16</sup> Besides the specimens on Pl. IV, fig. 3 the author has examined several other female gibbon fetuses and two nearly adult female *Symphalangus syndactylus*, all of which agreed very well with the above findings. In the siamangs the labia majora were covered with many short, black hairs, whereas the gibbon of Pl. IV, fig. 3, had fewer but longer hairs on these places. Pocock (1925) mentions that in two adult female *Hyllobates lar*, examined by him, "there were a few hairs on the labia of the vulva."



callosities can hardly be more than traced on the skin." An infantile male chimpanzee of the National Museum (No. 154,183, species not determined, sitting height 461 mm.), kindly lent to the author by Mr. G. S. Miller, Jr., possesses fairly large and quite conspicuous ischial callosities. In a great many other chimpanzees and oranges, examined by the writer, there was absolutely no trace of true callosities, but it was noted that the length and density of the hair in the zones overlaying the ischial tuberosities vary a great deal, quite a few of these specimens being nearly bare on these places without, however, showing any thickening and hardening of the skin.

In gorilla fetus IV Bolk found the hair in the region, in which these callosities could be expected, to be arranged in the form of spirals. In the slightly older chimpanzee fetus of the same author these places were entirely free of hair. The writer agrees with Bolk's interpretation of these findings, which is quoted herewith: "Die Bedeutung der haarfreien Stelle am Perineum des Schimpansen darf vielleicht eine nämliche sein als jene der beiden para-analen Spiralen beim Gorilla, eine Reminiszenz an die ebenfalls völlig haarfreien Gesässschwien niedriger Affen. . . . Bei menschlichen Embryonen lässt die Haarrichtung keine Andeutung derselben sehen."

The ischial callosities of catarrhine monkeys make their appearance before the lanugo develops on the caudal end of the trunk, there is, therefore, never any hair on the place of these callosities. Among fetuses of *Colobus* monkeys, for instance, no lanugo is present as yet in a specimen with a sitting height of 89 mm. but the callosities are already clearly indicated by a more pronounced smoothness and slightly greater thickness of the skin in these places than in the surrounding region. In four older *Colobus* fetuses, ranging in sitting height from 112 to 147 mm., the lanugo has appeared but does not extend over the areas, occupied by the developing callosities.<sup>17</sup> In contrast to these conditions in lower primates the callosities of the gibbon develop late, *i.e.*, considerably after the lanugo has started to develop and not until after their typical place has been temporarily covered by very fine hair. This mode of development was studied by the author especially on the splendid gibbon material (*Hylobates pileatus*) which the late Dr. R. A. Spaeth had generously collected for the Anatomy Department of the Johns Hopkins University. A fetus of 102 mm. sitting height showed neither lanugo nor callosities. In the next older specimen, measuring 158 mm., very fine and extremely short hair is seen under magnification to extend uninterruptedly over

<sup>17</sup> Three of these *Colobus* fetuses have been described by the author in a special paper (1924 b); the remaining two, which belong to the collection of the U. S. National Museum, were studied more recently.

the gluteal regions, including the zones overlying the ischial tuberosities. A fetus of *Hylobates mülleri* (161 mm.) showed exactly the same conditions and the gibbon fetus (vertex – coccyx = 136 mm.), described by Schmidt (1892), must have reached a similar stage of development judging by the following statement by this author: “. . . wenn man die Gesässpartie genauer mit der Loupe prüft, so erkennt man, dass diese ganze Region, und insbesondere auch die Stellen, wo die Gesässschwien sitzen würden, gleichmässig eine Anzahl feinsten Härchen, die nur Bruchteile eines Millimeters lang sind, trägt. Die Haut über den Sitzbeinknorren unterscheidet sich in nichts von der umgebenden Haut, und Callositäten an diesen Stellen lassen sich mit Sicherheit ausschliessen.” In a still older fetus of *Hylobates pileatus* (sitting height 169 mm.) there occurs the first indication of the ischial callosities in the form of two symmetrically placed hair-free zones, each about 3 mm. in diameter. The short hair surrounding these bare areas is directed toward their centers.<sup>18</sup> In the gibbon fetus of Deniker (1885), in which the hair was much more developed than in any of the above mentioned specimens, the bare ischial areas are considerably larger than in the oldest *H. pileatus* fetus, but not yet as large as in an infant of the same species, measuring 198 mm., or as in a new-born *H. lar* with a sitting height of 173 mm. Only in the last two specimens have the ischial callosities become horny or really callous.<sup>19</sup> Even in the infant, however, the callosities have not yet attained as relatively large a development as in adult gibbons.

With this rather lengthy digression the following conclusions seem justified. The ischial callosities are most strongly developed in the catarrhine monkeys, appearing very early in their ontogeny. In the gibbons they develop very much later, actually replacing a primary coat of hair. In the large apes they can occur in occasional specimens (in chimpanzee perhaps as a specific character?), the least tendency in this direction existing in gorilla, in which callosities are at best indicated by mere traces. That these callosities, when present in the apes, may become accentuated with advancing age through pressure and friction is not at all impossible. However, that these occasional callosities can not have been caused merely by mechanical action, as Friedenthal is inclined to believe, is evident at least from the

<sup>18</sup> The direction of the hair in this region may apparently vary, since Schwalbe (1911), in speaking of a gibbon fetus of 218 mm. vertex-coccyx length (measured with tape), makes the following remark: “Die kranio-kaudal gerichtete Behaarung des Rückens setzt sich in derselben Richtung neben dem After und den nur angedeuteten Gesässschwien auf das Glutealgebiet fort.”

<sup>19</sup> In the lower monkeys the thickening and subsequent hardening of the skin over the ischial tuberosities begins at a relatively much earlier stage of development. For instance, in two *Pithecius rhesus* fetuses of the author's collection (sitting heights 163 and 167 mm.) these callosities are already modified into horny layers. An enlarged reproduction of a section through the thick callosity of a baboon fetus can be seen in a publication by Anthony and Villemin (1923).



occurrence of hair-free zones over the ischial tuberosities in the prenatal life of chimpanzee, a condition which is identical with the first stage in the development of these callosities in the gibbon.

### Chapter 9. LIMBS.

All the proportions pertaining to the extremities of gorilla are collected in Table 4. In relation to the height of the trunk the length of the limbs changes comparatively little in the course of growth, at least as far as can be judged by the variable indices 10, 19, and 19a. Fetus III has the relatively longest limbs of the entire series, or rather the relatively shortest trunk. Disregarding this fetus, which in these proportions represents most likely an extreme variation, it appears that the relative length of the upper limb increases in general from early fetal to late infantile life, but reverses the trend of its growth thereafter to a slight secondary decrease. Expressed in figures this proportion (i 10) rises from 160 in fetus I to 191 in infant XII, but drops from there to 156 in the adult XVII. This constitutes a new confirmation of the following statement, made by the author in 1924 (a): The relative length of the upper extremity shows an initial increase in all primates, reaching its maximum at varying stages of growth and followed by a subsequent decrease which, however, in some forms, such as man, may change still later into a second rise. That the maximum in this relative measurement is attained before, and is also greater than in adult life, is shown by the following additional examples: Total length of upper limb in percentage of trunk height (i 10) in orang-utan: fetus (145 mm. sitting height) 195.5, infant 280.5, adult (7) 207.2; gibbon: fetus (4) 181.5, infant *H. pileatus* 219.0, infant *H. lar* 237.2, adult *H. leuciscus* 219.0, adult *H. lar* 230.8, adult *H. agilis* 232.3, adult *H. concolor* (8) 280.0; rhesus monkey: fetus (close to term) 167.6, adult 124.9; baboon: fetus (116 mm. sitting height) 129.0, new-born (225 mm. sitting height) 170.1, adult 140.0. The length of the lower extremity, whether including the height of the foot or not (i 19 & i 19a), shows a slight tendency to increase with advancing growth in its relation to the trunk height.

The proportion between the length of the upper and that of the lower limb (i 26 & i 27) is rather variable, but in spite of this, these indices show in general a slight decrease in the course of development, indicating that the lower extremity grows somewhat more intensely than does the upper one. If the total limb lengths are considered (i 26) the upper one amounts to more than 150 per cent of the lower one in the fetuses and infant, but to only about 140 per cent in the juvenile and adults. The intermembral index (i 27) formed only of the proximal and middle



limb segments is very high in the first and third fetuses, but very low in the second and fourth. The fact that fetuses I and II differ so much in the latter proportion, but so little in the former, can be traced directly to the difference in the relative length of the hand between the two fetuses, since the hand amounts to only 24.6 per cent of the total length of the limb (i 14) in fetus I but to 30.2 per cent in fetus II. The decrease of index 27 during postnatal life is best demonstrated on the average values derived from the exact and reliable measurements on skeletons. They amount in the infants (XI) to 123.7, in the juveniles (XV) to 118.6, and in the adults (XVIII) to 117.1 (See also Table 5). It may be mentioned here that an ontogenetic decrease in this proportion forms the rule in primates, but, whereas in most monkeys and apes the decrease is not very marked, it is very great in man. While discussing this particular index attention is called to its apparent tendency to differ in at least two of the species of gorilla. This difference is demonstrated in text-figure 1, and can also be seen in Table 5. The sum of the humerus and

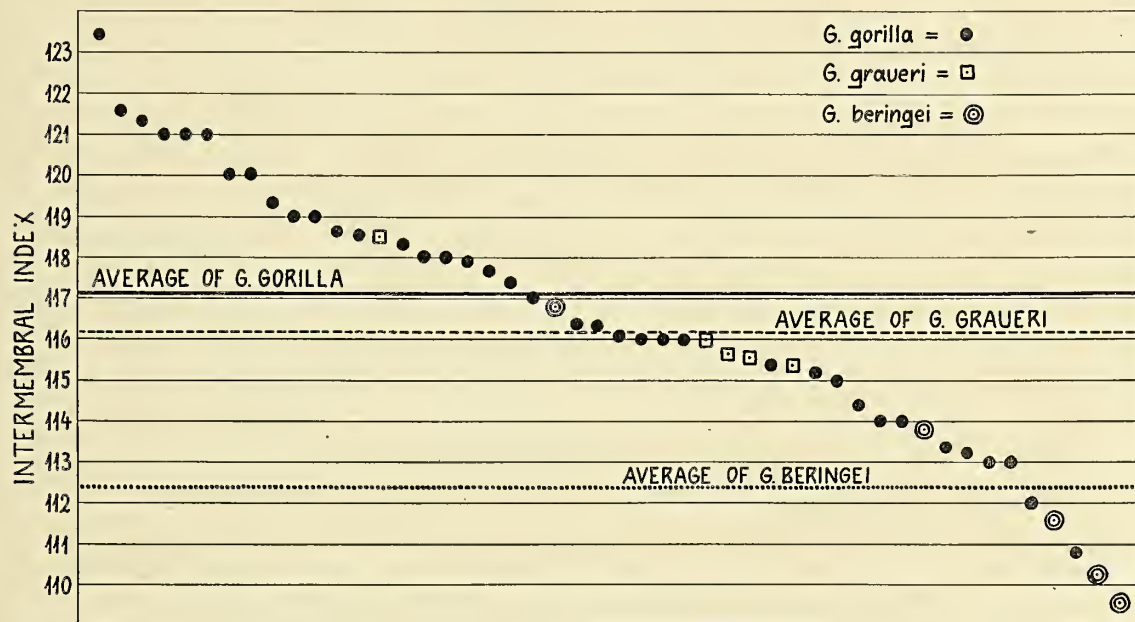


Fig. 1. Individual variations of the intermembral index (length of humerus+radius in percentage of length of femur+tibia) of thirty-eight adults of *Gorilla gorilla*, five adults of *G. graueri*, and five adults of *G. beringei*, grouped according to size of index. All these specimens are listed in Table 5.

radius lengths in percentage of the added lengths of femur and tibia averages in adult Lowland Gorillas 117.1 (with no noteworthy sex difference) and in the Highland Gorillas, (*Gorilla beringei*) 112.4. All the individual values of the latter fall below the average of the former, but the ranges of variation in the two groups overlap to a considerable extent. It can be said, therefore, that, whereas there exists no constant specific difference in this respect, *Gorilla beringei* shows never-

theless a clear trend toward having relatively shorter arms, or rather relatively longer legs, than *Gorilla gorilla*. The latter in this respect is removed somewhat further from man than is the former. In the author's opinion this distinction can be interpreted as indicating a greater adaptation to terrestrial life in the East African *Gorilla beringei* than in the West African forms. As will be pointed out later on, a study of the hands and feet in these two types of gorilla leads to corroborative conclusions. *Gorilla graueri* stands in regard to its intermembral index between *Gorilla gorilla* and *Gorilla beringei*, but, though a Mountain Gorilla, its average approaches that of the former more closely than it does that of the latter.

TABLE 4.  
Growth changes in the proportions of the limbs of gorilla.

Index No.	Percentage relation between:	Fetus I	Fetus II	Fetus III	Fetus IV	Infant VII	Infant VIII	Infant IX	Infant XI	Infant XII	Juven. XIII	Juven. XIV	Juven. XV	Adult XVI	Adult XVII	Adult XVIII
10.	Total upper limb l. (m.22) & Trunk h. (m.4).....	160.5	163.2	234.0	....	177.6	186.0	....	....	191.0	....	166.7	....	176.0	156.0	....
12.	Upper arm l. (m.23) & Total upper limb l. (m.22).....	39.6	37.7	38.4	....	37.7	37.8	37.8	....	39.7	....	42.7	....	39.0	40.6	....
13.	Forearm l. (m.24) & Total upper limb l. (m.22).....	35.8	32.1	34.1	....	33.8	31.6	35.8	....	32.6	....	32.1	....	35.4	33.6	....
14.	Hand l. (m.25) & Total upper limb l. (m.22).....	24.6	30.2	27.5	....	28.5	30.6	26.4	....	27.7	27.1	25.2	....	25.6	25.8	....
15.	Forearm l. (m.24) & Upper arm l. (m.23).....	90.5	85.2	82.2	92.6	89.5	84.0	94.5	83.8	82.0	....	75.2	81.2	90.9	82.9	80.8
16.	Hand l. (m.25) & Forearm l. (m.24).....	68.4	93.9	80.9	....	84.3	97.0	73.7	....	85.0	....	78.6	....	72.0	76.5	....
17.	Thumb l. (m.26) & Hand l. (m.25).....	....	48.0	....	....	....	....	....	....	....	....	60.6	....	42.7	....	....
18.	Hand b'dth (m.27) & Hand l. (m.25).....	....	39.0	....	....	....	....	....	....	....	....	46.7	....	36.6	....	....
19.	Total lower limb l. (m.15) & Trunk h. (m.4).....	103.0	107.9	....	....	115.3	....	....	....	....	....	119.2	....	126.2	110.8	....
19a.	Thigh l. + leg l. (m.16 + 18) & Trunk h. (m.4).....	91.0	99.5	138.8	....	....	111.0	....	....	115.0	....	108.4	....	118.6	100.0	....
21.	Leg l. (m.18) & Thigh l. (m.16).....	76.5	78.8	79.5	70.4	....	83.0	96.2	83.1	83.0	....	75.2	81.5	82.7	88.4	80.2
22.	Foot l. (m.19) & Leg l. (m.18).....	115.3	106.7	133.2	....	....	116.0	107.8	....	112.0	98.5	107.1	....	100.0	97.6	....
23a.	Foot l. (m.19) & Vertex-coccyx l. (m.1 a).....	21.1	22.1	32.6	....	34.7	....	33.8	....	....	....	30.3	....	....	35.0	....
24.	Foot b'dth (m.21) & Foot l. (m.19).....	46.7	31.6	29.6	....	....	....	34.3	....	....	....	31.4	....	....	....	....
26.	Total upper limb l. (m.22) & Total lower limb l. (m.15).....	155.8	151.2	....	....	154.0	....	....	....	....	....	139.6	....	139.5	140.7	....
27.	Upper arm + forearm (m.23 + 24) & Thigh + leg (m.16 + 18).....	133.3	114.5	123.3	113.0	125.5	121.0	123.8	123.7	116.0	111.6	115.0	118.6	110.4	115.8	117.1
28.	Upper arm l. (m.23) & Thigh l. (m.16).....	123.4	110.6	121.5	100.0	....	115.0	125.0	123.2	120.0	....	114.9	118.9	105.7	119.2	116.7
29.	Forearm l. (m.24) & Leg l. (m.18).....	146.1	119.6	125.6	131.5	....	118.0	122.8	124.3	119.0	....	115.0	118.5	116.2	111.9	117.5
30.	Hand l. (m.25) & Foot l. (m.19).....	86.7	105.2	86.4	....	80.3	96.0	84.0	....	91.4	83.4	84.3	....	83.7	80.4	....

Of the three segments of the upper limb the upper arm is the longest and the hand the shortest at all stages of growth. The percentage participation of the lengths of upper arm, forearm, and hand in the formation of the total limb length shows no noteworthy and clear change with advancing growth, except that the relative hand-length has somewhat higher values among fetuses and infants than in the adults. (See i 12, i 13, and i 14 in Table 4). Attention must here be called to the interesting fact that the segments of the upper limb have practically the



same proportionate lengths in adult gorilla as in adult man. Adult chimpanzee, orang-utan, and gibbon constitute a quite different group in this respect, since they have relatively shorter upper arms and relatively longer hands than the former two primates. As shown by Table 8, the upper arm amounts to 41 per cent of the total upper limb length in adult gorilla and in man, but to only 35 to 36 per cent in the other higher primates and the hand forms about 25.5 per cent of the total limb length in the former two, but 28.4 to 29.5 per cent in chimpanzee, orang, and gibbon.

TABLE 5.

Proportions between the long bones of the limbs of gorilla skeletons. Infants = series XI, juveniles = series XV' adults (*G. gorilla*) = series XVIII in chapter on material. All these gorillas are West African Lowland Gorillas, belonging in all probability to the various subspecies of *G. gorilla* (see Elliot, 1913). *Gorilla graueri* and *Gorilla beringei* are Mountain Gorillas from Central and West Africa. The proportions (from left to right) correspond very closely to the following indices in Table 4: i 15, i 21, i 27, i 28, and i 29.

				Percentage Relation Between					
Species	Age	Sex	Collection or Author	Humerus	Radius	Tibia	Hum.+ Rad.	Humerus	Radius
				length	Humerus	Femur	Fem.+ Tib.	Femur	Tibia
<i>G. gorilla</i>	infant	?	Bolk, L. 1926.....	152	86.2	81.6	124.7	121.6	128.4
"	"	"	Deniker, J. 1885.....	170	81.8	85.2	123.5	125.9	120.8
"	"	"	Western Reserve University....	181	83.5	82.5	122.9	122.2	123.8
"	Juvenile	"	Bolk, L. 1926.....	240	86.7	77.7	117.3	111.6	124.5
"		"	Mollison, T. 1911.....	266	79.0	82.0	120.0	122.0	118.0
"		"	Johns Hopkins University.....	276	77.9	84.8	118.5	123.1	113.1
"	adult	♀	Western Reserve University....	344	84.7	78.7	120.0	116.1	124.8
"		"	Mollison, T. 1911.....	353	81.0	84.0	116.0	119.0	113.0
"		"	Lorenz v. Liburnau, L. 1917....	354	79.4	80.5	118.0	118.7	117.0
"		"	Mollison, T. 1911.....	356	80.0	80.0	121.0	122.0	122.0
"		"	Western Reserve University....	357	82.4	81.1	119.3	118.5	120.4
"		"	Johns Hopkins University.....	357	78.2	82.3	116.3	118.9	112.8
"		"	U. S. National Museum.....	357	79.3	78.7	118.3	118.5	119.3
"		"	Mollison, T. 1911.....	359	83.0	80.0	121.0	119.0	123.0
"		"	Western Reserve University....	360	84.2	83.3	121.3	120.7	122.1
"		"	Dealer's Store, Berlin.....	362	80.1	78.7	121.6	120.6	122.8
"		"	Mollison, T. 1911.....	365	82.0	85.0	113.0	115.0	111.0
"		"	Deniker, J. 1885.....	370	81.5	78.0	110.8	108.5	113.8
"		"	Mollison, T. 1911.....	378	81.0	83.0	113.0	115.0	112.0
"		"	Bolk, L. 1926.....	380	80.3	78.6	118.7	117.6	120.0
"		"	Mollison, T. 1911.....	382	79.0	81.0	117.0	119.0	116.0
"		"	American Museum of Nat. Hist..	403	77.4	78.1	114.0	114.4	113.4
AVERAGE OF ADULT FEMALES.....				365	80.8	80.7	117.5	117.6	117.7
<i>G. gorilla</i>	adult	♂	U. S. National Museum.....	403	77.9	78.3	114.4	114.7	114.1
"	"	"	Mollison, T. 1911.....	403	79.0	78.0	119.0	116.0	118.0
"	"	"	American Museum of Nat. Hist..	407	81.6	80.6	118.6	117.9	119.4
"	"	"	Mollison, T. 1911.....	412	78.0	79.0	116.0	117.0	115.0
"	"	"	American Museum of Nat. Hist..	421	80.3	79.7	117.7	117.2	118.1
"	"	"	Johns Hopkins University.....	424	78.9	79.5	115.4	115.8	115.0
"	"	"	Mollison, T. 1911.....	424	79.0	78.0	120.0	118.0	121.0
"	"	"	Western Reserve University....	425	85.2	77.3	117.3	112.3	123.8
"	"	"	Lorenz v. Liburnau, L. 1917....	427	83.4	82.3	113.3	112.6	114.0
"	"	"	Mollison, T. 1911.....	427	83.0	77.0	112.0	109.0	116.0
"	"	"	Mollison, T. 1911.....	428	80.0	79.0	118.0	118.0	119.0
"	"	"	Mollison, T. 1911.....	428	83.0	78.0	121.0	117.0	125.0



Species	Age	Sex	Collection or Author	Humerus length	Radius Humerus	Percentage Relation Between			
						Tibia Femur	Hum.+Rad. Fem.+Tib.	Humerus Femur	Radius Tibia
<i>G. Gorilla</i>	adult	♂	Columbia University.....	432	80.5	80.5	115.2	115.1	115.1
"	"	"	U. S. National Museum.....	433	81.3	78.3	117.9	116.0	120.4
"	"	"	Mollison, T. 1911.....	434	83.0	84.0	114.0	114.0	113.0
"	"	"	Mollison, T. 1911.....	435	85.0	77.0	119.0	115.0	126.0
"	"	"	Mollison, T. 1911.....	437	82.0	81.0	115.0	114.0	116.0
"	"	"	Lorenz v. Liburnau, L. 1917....	440	80.0	85.8	116.1	119.8	111.7
"	"	"	Mollison, T. 1911.....	441	81.0	79.0	116.0	115.0	117.0
"	"	"	Bolk, L. 1926.....	452	83.6	80.1	113.2	111.0	115.8
"	"	"	Du Chaillu, P. B. 1861.....	457	75.7	80.0	123.4	126.5	119.6
"	"	"	Western Reserve University....	460	75.7	83.1	116.3	121.3	110.4
AVERAGE OF ADULT MALES.....				430	80.8	79.8	116.8	116.1	117.4
AVERAGE OF ADULT MALES AND FEMALES ( <i>G. gorilla</i> )....				402	80.8	80.2	117.1	116.7	117.5
<i>G. graueri</i>	adult	♀	Lorenz v. Liburnau, L. 1917....	372	75.5	77.8	116.0	117.6	114.2
"	"	"	Lorenz v. Liburnau, L. 1917....	385	74.5	76.0	115.6	116.6	114.3
"	"	♂	Lorenz v. Liburnau, L. 1917....	428	79.2	77.0	118.5	117.2	120.5
"	"	"	Lorenz v. Liburnau, L. 1917....	447	76.3	78.5	115.4	117.0	113.6
"	"	"	Lorenz v. Liburnau, L. 1917....	465	75.5	80.7	115.7	119.2	111.3
AVERAGE OF ADULT MALES AND FEMALES ( <i>G. graueri</i> )...				419	76.2	78.0	116.2	117.5	114.8
<i>G. beringei</i>	adult	♀	American Museum of Nat. Hist.	344	85.0	79.8	113.8	110.5	117.7
"	"	"	American Museum of Nat. Hist.	362	83.5	85.9	109.6	111.0	107.8
"	"	♂	American Museum of Nat. Hist.	390	88.5	79.3	110.2	104.7	116.8
"	"	"	American Museum of Nat. Hist.	412	87.4	83.1	111.6	108.9	114.6
"	"	"	U. S. National Museum.....	435	83.2	79.5	116.8	114.4	119.8
AVERAGE OF ADULT MALES AND FEMALES ( <i>G. beringei</i> )...				389	85.5	81.5	112.4	109.9	115.3

It is almost impossible to recognize a definite growth change in the proportion between forearm and upper arm (i 15) since the values for this index vary individually to a very marked extent. In general it may be said that this proportion shows a slight tendency to decrease with advancing growth. The forearm length of the small series of fetuses fluctuates between 82.2 and 92.6 per cent of the upper arm length, a range which is even surpassed by that of the adults (58 specimens) among which the radius-humerus proportion varies according to Tables 5 and 6 between 74.5 and 88.5. The latter range reaches far into the field of human variations since in individual cases the humero-radial index of adult man may be as high as 85.1, a value found by Sarasin (1916-1922) in a male Loyalty Islander, or reach an extreme of 87.6, obtained by the writer on the skeleton of an adult American negress. Fick (1926) has recently published the humero-radial index of ten adult gorillas, of which, however, he gives neither species nor sex. Judging by the length of the humerus, the majority of these specimens must be male. This series is listed separately in Table 6. If all the material of adult gorilla skeletons in Tables 5 and 6 is combined, an average humerus-radius proportion in these 58 specimens is obtained as 80.69 with a probable error of  $\pm 0.26$ . According to Martin (1914) the averages of this proportion range among human races from

71.3 to 81.5 and the average of the values for the 63 groups, listed by this author, amounts to 76.74. Man is characterized by having on an average the relatively shortest forearm of all primates (Mollison, 1911; Schultz, 1924 a & 1926 b), but gorilla, in this respect, ranks a close second. It may be mentioned also that, as there are marked racial differences in this proportion in man, so there are apparently differences between the species of gorilla, since *Gorilla graueri* has an average humero-radial index of 76.2, *Gorilla gorilla* one of 80.8, and *Gorilla beringei* one of 85.5. The difference between the first and the last mentioned form is indeed very striking, and particularly significant, since the ranges of variation do not overlap. On the basis of these figures it can be stated that at least one form of gorilla (*G. graueri*) has on an average as relatively short a forearm (76.2 per cent of upper arm length) as the average man (76.7 per cent of upper arm length). Chimpanzee, orang-utan, and gibbon, on the other hand, are far removed from man in this respect, since their forearms approach or even surpass their upper arms in length.

TABLE 6.

Radius length in percentage of humerus length in ten adult gorillas, according to Fick (1926).

Humerus lengths	Radius in pr. ct. of Humerus
352 mm.	80.7
387 "	79.3
420 "	81.9
420 "	83.3
445 "	80.9
445 "	81.1
460 "	78.3
460 "	77.2
469 "	78.9
478 "	79.1
Average	80.1

The percentage relation between leg length and thigh length (i 21) falls below 80 in the fetuses, but above that value in postnatal life, with the exception of the juvenile XIV. If the scanty and variable data for this proportion permit any conclusion at all, it can be stated in a preliminary way, that in general the leg seems to exceed the thigh in rate of growth, a condition which conforms with that prevailing in most primates, including man.

At several places above reference was made to the marked individual variations in body proportions of gorilla. The figures of Table 5 furnish an opportunity to add here some further comment on the variability of this ape. In the thirty-eight skeletons of adult *Gorilla gorilla* the humero-radial index ranged from 75.7 to 85.2, the femoro-tibial index from 77.0 to 85.8, the intermembral index from



110.8 to 123.4, the humero-femoral index from 108.5 to 126.5, and the radio-tibial index from 110.4 to 126.0. These wide ranges all indicate a variability which is at least equal to, if not at times larger than the variability of the same proportions in man. Sir Arthur Keith (1926) has recently stated that gorilla varies individually more than does man. Although the writer is not prepared to endorse this view unconditionally, he is convinced that gorilla is at least fully as variable as man.<sup>20</sup> This last conclusion is justified in regard to the limb proportions and is undoubtedly true also in regard to the skull of gorilla, as was shown for instance by the studies of Selenka (1899), Duckworth (1904 b), Bolk (1925), and Harris (1926).

*The hand and the foot.* The last part of this chapter will be devoted to the consideration of the distal segments of the limbs, the hand, and the foot. In only one (fetus II) of the specimens listed in Table 4 does the hand exceed the foot in length (i 30). Other indices in this table permit a more exact analysis of this exception, since it can be shown that it is not so much the foot which is unusually short (i 22 & i 23a), but that it is the hand which has a greater relative length (i 14 & i 16) than in any of the other gorilla fetuses. The percentage relation between hand and foot lengths of fetus II, amounting to 105.2, represents, therefore, in all likelihood not a typical step in the growth changes of this proportion but a rare variation. In the younger as well as in the older fetus (I & III) this index is much lower, namely 86.7 and 86.4. In all adults the hand is shorter than the foot in gorilla just as in the majority of other primates and particularly in man. A reversed relation exists chiefly in the gibbons, but also in some chimpanzees.

Fick (1926) has already pointed out that the hand of adult gorilla is unusually short in relation to the length of the upper limb (without hand). According to this author the hand length in percentage of the added humerus and radius lengths amounts to 31.7 and 33.2 in two adult gorillas, whereas in sixty-two human adults it averages 33.7, in two adult orangs 35.4, and in three adult chimpanzees 43.5. The writer's results agree very closely with these findings of Fick, since the same proportion (but taken on the outer body, instead of on the skeleton) was found to average 34.1 in 24 adult white men (series 5), and to be 34.4 in gorilla XVI and

<sup>20</sup> It must be borne in mind that our knowledge of the variability of a species depends to a great extent upon the number of specimens examined. Naturally, much larger series are available for the study of variability in man than for that in gorilla; so it is all the more surprising that even the comparatively scanty material of the latter reveals so wide a range of variation.

For the humerus-radius proportion of the combined series of fifty-eight adult gorillas, listed in tables 5 and 6, the standard deviation and its probable error amount to  $2.93 \pm 0.19$  and the variation coefficient to  $3.64 \pm 0.23$ . The degree of variability, indicated by these figures, becomes apparent from a comparison of them with the values of these coefficients for the very similar upper arm-forearm index of 100 adult whites, as given by Mollison (1911): Standard deviation  $2.79 \pm 0.13$ , variation coefficient  $3.56 \pm 0.17$ .



34.7 in gorilla XVII, 39.6 in an adult orang (7), 39.9 in an adult gibbon (8), and 41.8 in an adult chimpanzee (6) (See also i 14, Table 8). In young gorillas this relatively short hand length is as a rule not yet so pronounced. For instance, it amounted to 37.0 in one juvenile (Fick). This is furthermore demonstrated by the fact that the indices 14 and 16 in Table 4 show higher values among fetuses and infants than in adults. There can be no doubt that a relatively long hand is an arboreal character and hence typically simian, whereas a short hand is decidedly non-arboreal and much better adapted to a terrestrial mode of life. It is particularly interesting and suggestive, therefore, to find that gorilla has a non-arboreal hand length and that this condition becomes most pronounced during late ontogenetic development.

In all primates studied so far the embryonic hand is proportionately broad and the hand width decreases in relation to the total hand length during at least some periods of growth (Schultz, 1926 b). As shown on Pl. V the hand of gorilla is already quite slender in fetal life, but, curiously enough, it changes in later growth into a much broader shape. A cast of the hand of the three-year-old female gorilla, "Dinah", kindly lent to the author by Prof. McGregor, has a much slenderer form than the hands of the two adult gorillas, shown on Pl. V.<sup>21</sup> Relatively even broader than the last two is the hand of an adult male Mountain Gorilla, pictured by Akeley (1923). The statement of Du Chaillu (1861) that "the hand of the gorilla is almost as wide as it is long" must have reference to the palm alone, and not to the entire hand including the digits, but shows also that in adult gorillas the hand has become very broad; indeed, fully as much so as in man, and much more so than in any of the other primates. It is very significant that among monkeys the relatively broadest hand is found in the largely terrestrial baboons (Schultz, 1924 a).

The thumb of all the primates, previously studied by the author (1926 b), becomes relatively shorter with advancing growth, and man at all ages retains a proportionately longer thumb than do monkeys and apes. In extremely arboreal primates the thumb is short or even tends to disappear entirely. In gorilla the thumb is unquestionably relatively shorter and also relatively thinner in fetuses than in adults (See Pl. V, and also Pl. II, fig 1). In the former the thumb reaches not quite to the base of the index finger, whereas in the latter it reaches easily to that place or even as far as the distal third of the basal phalanx of the second

<sup>21</sup> The length-breadth proportion of the hand (i 18) of Lowland Gorillas amounts to 39.0 in fetus II, to approximately 35.0 in the three year old "Dinah", to 36.6 in the adult female XVI, and to 49.5 in the adult of Hartmann, but in Highland Gorillas to 46.7 in the juvenile XIV, to approximately 60 in the adult female, shown on Plate V, and to roughly 64 in the adult male of Akeley. Judging by these meagre data *Gorilla beringei* has a relatively broader hand than has *Gorilla gorilla*, and one even broader than have most human beings.

finger. In the Mountain Gorilla the thumb seems to have a greater relative length than in the Lowland Gorilla, judging by the fact that the young *Gorilla beringei*, XIV, has an index (17) of 60.6 and the adult *Gorilla gorilla* XVI one of only 42.7. This seems furthermore evident from a comparison of the two adult hands on Pl. V. In chimpanzee and orang the thumb is much weaker and reaches as a rule not as far as in gorilla. It is, therefore, again the latter ape which stands closest to man in the relative size of the thumb.

It must be mentioned also that the degree of rotation, *i.e.*, of opposability, of the thumb, varies a great deal in gorilla. As shown on Pl. V, the transverse axis of the thumb (determined by the nail) stands nearly parallel to that of the other digits in fetus II and the adult of Hartmann, but is rotated very considerably in fetus III and the adult of Akeley, the nail being plainly visible from the palmar side of the hand in the latter two, in which the thumb appears to be as opposable as in adult man.

These notes on the thumb and on the relative hand width tend to strengthen still further the argument advanced in connection with the above discussion of the relative hand length. It can all be summarized in the statement that gorilla possesses a relatively short and very broad hand with a proportionately strong and long thumb, all characters which are decidedly less arboreal than in the other apes and in which gorilla closely approaches, equals, or even surpasses man. The fact that the fetal and infantile hands are in all these points more simian than the adult hand suggests strongly the possibility that gorilla has become less adapted for arboreal life only in comparatively recent stages of its evolution. It is particularly interesting that this apparent emancipation from tree-life, if one may conclude from the conditions of the hand, seems to have advanced further in the Mountain Gorilla than in the lowland forms.

To this discussion on the hand of gorilla may be added some notes and quotations appertaining to a very interesting peculiarity in the knuckles of the African anthropoids. This seems particularly desirable since these scattered observations have never before been collected. Du Chaillu (1861), in speaking of the gorilla, states: "The skin on the back of the fingers, near the middle phalanx, is callous and very thick, which shows that the most usual mode of progression of the animal is on all-fours, and resting on the knuckles." The same can be said in regard to chimpanzees, which also support themselves on their flexed fingers, particularly on the middle phalanges, whereby most pressure is exerted on the joint between the basal and middle digital segments. Neither gorilla nor chimpanzee has any hair on the middle portions of its fingers, whereas the gibbon, for instance,



which does not use its knuckles in walking, does have hair on these places. The following rather unexpected findings on fetuses of African apes are especially significant in this connection. Referring to gorilla fetus IV Bolk (1926 b) mentions: "Was die Finger betrifft, war der Daumen auch bei diesem Embryo noch ganz unbehaart, von den übrigen Fingern war der Grundphalanx behaart wie beim Schimpansen, und überdies fanden sich auf den Endphalangen fünf bis sechs etwas straffe Härchen, die beim Schimpansen fehlten. Die eigentümliche Erscheinung, dass Grund- und Endphalanx wohl, Mittelphalanx dagegen nicht behaart ist, darf vielleicht erklärt werden durch die Tatsache, dass die Haut der proximalen Hälfte der Mittelphalangen ein wenig polsterartig hervorsprang infolge einer kräftigen Entwicklung der Epidermis. Die Oberfläche des Überganges von Mittel- in Grundphalanx schien wie mit kleinen Schwielenhöckern besetzt. Beim Schimpansen vermisste ich diese Bildungen." Though Bolk's chimpanzee fetus did not possess these "phalangeal callosities", they can occur in this ape at prenatal stages, as was shown by Friedenthal (1908 a), who made the following observation on a chimpanzee fetus, which is not as far advanced in development as Bolk's specimen: "Als auffälligen Befund zeigte der untersuchte Fötus des Tschego bereits haarlose Schwielen an den Fingern trotz Behaarung des Nagelgliedes der Finger. Die durch das Laufen auf den umgeschlagenen Fingern erworbenen Schwielen der anthropoiden Affen sind daher durch Vererbung in der gleichen Weise fixiert wie die Liegeschwielen der Kamele."

There can be no doubt that, connected with their special mode of walking, gorilla and chimpanzee have lost the hair on the middle phalanges of their fingers, show a thickening of the skin on these places with a tendency to its becoming callous, and that these peculiarities are at least in some instances present before birth. This, as was pointed out by Friedenthal, is directly comparable to the early ontogenetic appearance of certain callosities in camels. Further very similar conditions are found in the warthogs (*Phacochærus æthiopicus*) which are in the habit of kneeling on their carpal joints and thus sliding around while digging for roots. The places on which they kneel are protected by thick callosities, which already develop during fetal life (Weber, 1904, and others). The author is not concerned here with the question whether these conditions can be used as support for the theory of inheritance of acquired characters or whether they should be regarded as "favorable mutations", or, possibly, receive a still different interpretation.<sup>22</sup> Whatever explanation one may favor, one must bear in mind that the

<sup>22</sup> It may be mentioned here that according to Lowe (1926) the "sternal callosities" of the ostriches, which are present in the embryo and which differ histologically from true callosities, are reptilian-derived characters and can not be considered as inherited acquired characters.



callosities, discussed above, are of the same nature, though not nearly as strongly developed, as the ischial callosities. Thomson (1907) after referring to the same observations on warthogs, which are mentioned above, concludes with the following statement: "This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character. It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection."

The interesting growth changes in the gorilla's foot are illustrated on Pl. VI. The length-breadth proportion of the foot decreases during early fetal life. This index (i 24, Table 4) amounts to 46.7 in the youngest known gorilla fetus,<sup>23</sup> but has dropped to 31.6 in fetus II and to 29.6 in fetus III. It is approximately the same as in the last fetus in the three year old female gorilla "Dinah" (according to a cast of its foot, kindly lent to the author by Prof. McGregor) and in the five year old male, shown on Pl. VI. In the juvenile Mountain Gorilla XIV this index amounts to 31.4 and is, therefore, also still about the same as in fetus II. As adult life is approached the foot of some gorillas may become extremely broad, as shown by the adult of Brehm on Pl. VI. That the relative breadth of the foot of adult gorilla is at least as great as that of man and greater than that of other apes is shown by the following values for the index 24: average in adult man (according to Table 8) 28.0, Akeley's cast of the foot of an adult Mountain Gorilla approximately 29.7, cast of the foot of an adult chimpanzee approximately 25.5, adult orang-utan 23.8, adult gibbon 21.6 (the last two values according to Table 8).

The relative length of the great toe, *i.e.*, the place on the second toe to which it will reach when adduced, varies in gorilla to such an extent that it is impossible to recognize any definite marked growth change in this condition. The distance from the heel to the tip of the great toe measures about 82 per cent of the total foot length in fetus I; in fetus II this proportion amounts to 89.0, if the hallux is adduced; in fetus III to about 87; in the three year old "Dinah" to approximately 74; in the three-and-a-half year old "John Daniel II" (measured alive by the author) to 83.8; in the five year old specimen of Pl. VI to about 82; and in the adult of Hartmann to about 85. The same proportion amounts to 93.8 in the juvenile Mountain Gorilla XIV, and to about 92 in the adult Mountain Gorilla of Akeley. It is very noteworthy that both the latter values are considerably higher than those of any of the above enumerated Lowland Gorillas. A corresponding difference in species is obtained from measurements taken of the skeleton of the foot, as demonstrated by the following figures kindly supplied to the author by Dr. W. L.

<sup>23</sup> The outline drawing by Duckworth of the foot of fetus I (copied exactly on Pl. VI) is evidently foreshortened in a transverse direction, since from this drawing one would obtain a much smaller relative foot breadth than that derived from the direct measurements by the same author.

Straus, Jr.: Distance from tuber calcanei to tip of hallux in percentage of greatest length of skeleton of foot in *Gorilla gorilla*, infant (sex unknown) 79.5, two adult males 78.9 and 83.3; in *Gorilla beringei*, infant male 87.6, adult male 90.7. If it now can be stated that the great toe reaches further in the Mountain Gorilla than in the West African forms, it does not imply that the phalangeal part of this toe is longer in the former than in the latter. From a comparison of the feet of the adults of Akeley and of Brehm on Pl. VI it seems much more likely that the free portion of the great toe is considerably shorter, and hence the metatarsal or tarsal portion relatively longer in *Gorilla beringei* than in *Gorilla gorilla*. In consequence of this relatively short free portion of the great toe in the Mountain Gorilla the cleft between the latter toe and the second toe is also proportionately short; indeed, it is of relatively shorter length than in some few human feet. For instance, the length of this cleft (distance *A1* or *A* to *B* on Pl. VI) in percentage of the total foot length (distance *A* to *C*) amounts to 22.0 in the adult Mountain Gorilla, to 22.5 in the negro fetus with the relatively longest toes, shown on the plate and to even 23.6 in one out of twenty-six adult white males, measured by the author. In *Gorilla gorilla* this cleft has at all stages of growth a considerably greater relative length, but not nearly as great as in orang-utans.

For an interpretation of these notes on the great toe of gorilla the author must repeat what he has stated in a previous paper (1926 b): Among adult monkeys the great toe branches from the sole at a varying but always considerable distance from the base of the second toe. Among adult anthropoid apes this feature differs least from the human condition in the Mountain Gorilla, and most in orang-utan, with a greater discrepancy between the latter two than between gorilla (particularly the East African form, but holding true also in regard to the West African forms) and man. There can be no question that the opposability of the great toe is greatly facilitated by its branching at a place which is removed from the second toe, so that, in the act of grasping, these two toes together with the intermediate medial edge of the sole form diagrammatically a U, rather than a V, as in man.

The lateral toes II to V are relatively short in the gorilla, when compared with the orang and gibbon, but in the West African gorilla relatively long in comparison with man. In many individual cases these two toes are united by webs of varying length (See *e.g.* the adult of Brehm on Pl. VI), as has been reported by a number of authors from Du Chaillu in 1861 to Straus in 1926. The transverse flexure folds on the foot have been carefully compared and marked by numbers on Pl. VI. The folds 1 and 2 are caused, or at least accentuated, by flexion in the metatarso-phalangeal joints, which are situated between these folds and, as a rule, slightly closer to fold 2 than to fold 1. The folds at 3 correspond fairly



accurately to the joints between the basal and middle phalanges. Of these crease-lines that marked 1 is in the gorilla sometimes missing (adult of Brehm) or only partly developed (adult of Akeley), whereas in man it is never present and line 2 is generally but faintly indicated or also missing. It is very interesting to find by means of these flexure-lines as landmarks that the sole of man has crept further distally along the lateral toes than in most gorillas. In the former the planta proper reaches in general all the way to line 3, though in individual cases it may not yet extend so extremely far on the second and third toes. In the majority of West African gorillas, on the other hand, the sole reaches only to line 2, as in fetuses I and II and in the adult of Brehm, or beyond that line but not to fold 3, as in fetus III and the adult of Hartmann. It is possible, but not very likely, that the portion of the "sole", which in the latter cases extends beyond line 2, should be regarded as webbing between toes. However, by comparing the adults of Brehm and of Hartmann it seems much more probable that the former represents a clear case of webbed toes, whereas the latter represents one with a distally extended sole. At any rate, there can be no doubt as to the nature of this condition in the adult Mountain Gorilla of Akeley. In this specimen the region between folds 2 and 3 appears so evenly padded, that it forms one continuous pillow-like structure, differing in no respect from the part between the creases 1 and 2. Here one certainly does not deal with any web formation, but with a true sole, which has migrated to the proximal end of the middle phalanges, just as in man. In consequence of this extreme forward extension of the sole, which has no parallel among other apes or monkeys, the lateral digits of the adult Mountain Gorilla are separated to an even lesser extent than in many human feet, such as for instance the foot of the negro fetus with maximum relative length of toe, shown on Pl. VI. These short free toes of gorilla, particularly *Gorilla beringei*, form a striking contrast to the exceedingly lengthened, over-developed toes II to V of the adult orang. As those of the latter are justly regarded as an ideal adaptation to arboreal life, so must the short toes of the former be interpreted as unsuitable for effective tree-climbing and as being more in accord with terrestrial habits.

The heel of gorilla is in most cases quite prominent, projecting beyond the profile of the ankle region. This condition may be very pronounced even in the fetus, as for instance in the specimen of Deniker, shown on Pl. II, fig. 2. Du Chaillu (1861) states that "the heel in the gorilla makes a more decided backward projection than in the chimpanzee." The relative degree of prominence of the heel was observed by the author as "very prominent" in two plaster casts of gorilla feet and in one live gorilla; "fairly prominent" in another cast of the foot of a gorilla; among ten preserved chimpanzees and one plaster cast of the foot of a chimpanzee as "fairly

prominent" in five cases, and as "not prominent" in the remaining six instances; among fourteen preserved orang-utans and one plaster cast of an orang foot as "very prominent" in one case, "fairly prominent" in four cases, and as "not prominent" in ten cases. Finally, it may be mentioned that in gibbons and monkeys the heel is never prominent, and that in man there exist marked racial differences in this respect (Schultz, 1926 b), since negroes possess a much more pronounced prominence than whites. While the gorilla equals man in regard to the prominence of its heel, it surpasses man in the relative width of the heel region of the sole. The juvenile and adult gorilla feet on Pl. VI show clearly that the sole of this ape does not become so narrow in the heel region as it does in the human foot, but is of nearly equal width underneath and behind the ankle as at the metatarsophalangeal joints. In gorilla fetuses this is not yet the case, since the region of the heel still tapers to a narrow, almost pointed shape.

The conclusions to be drawn from this discussion of the foot of the gorilla are very similar to those derived from the study of the hand. Like the hand, the foot is still more typically simian and arboreal in fetal stages of development than at the completion of growth. Fetus II supplies the best example of this. In this specimen the phalangeal portions of all the toes are relatively long, the great toe branches from the sole proportionately far from the base of the second toe, and the heel is narrow and rather pointed, all features characteristic of a climbing foot, though not developed to such extremes as in the orang and gibbon. The foot of the adult Mountain Gorilla seems to be built according to a quite different plan. Here the free digits are very short and can not possibly be as mobile as the long and slender fetal toes. The great toe is relatively thicker and stronger, reaching more distally than in the fetus, and branching from the sole further forward, *i.e.*, at flexure fold 2 instead of 1 as in the younger stages. Finally, the heel has become very broad in the adult, forming a huge pad, ideally adapted for supporting the enormous weight of the body while walking on the ground. Some of these features, chiefly the relative lengths of the toes, have not departed so much from the arboreal type in the adult Lowland Gorilla as in the adult *Gorilla beringei*.

Without knowing anything of its habits one might deduce from the conditions of the foot of adult *Gorilla beringei* that this ape, the heaviest of all primates, must at best be but poorly adapted for climbing in trees. Such a conclusion is fully borne out by the following statement of Akeley (1923), who has had such enviable opportunities to study the Mountain Gorilla in its native environment: "I believe that he has nearly passed out of the arboreal phase of life and is perhaps entering the upright phase and that he is the only animal, except man, that has



achieved this distinction. To stand erect and balanced, an animal needs heels. The plaster cast of the gorilla's foot . . . is evidence . . . that the gorilla has developed a heel." Later on Akeley adds: "The German, E. Reichenow, who observed gorillas in this same area, agrees that the gorilla is seldom in trees."

### Chapter 10. HEAD.

In all higher vertebrates the head becomes proportionately smaller with advancing growth. That the gorilla conforms to this rule is demonstrated by the indices 31 a and 33 a in Table 7. The average diameter of the head may, for instance, amount to nearly 90 per cent of the height of the trunk in a fetus, but to only 40 per cent in a juvenile. The side views of the heads of gorillas on Pl. VII show the decrease of the relative height of the head (ear opening to vertex) and the closely connected rapid lowering of the forehead with advance in growth. The gorilla fetuses I and II differ relatively little in regard to these points from the negro fetuses I and II, but in later stages of development the forehead of gorilla is much lower than the human forehead and the entire sagittal curvature of the brain-case has become flatter.<sup>24</sup> This is also evident from the growth change in index 34a.

TABLE 7.  
Growth changes in the proportions of the head of gorilla.

Index No.	Percentage relation between:	Fetus I	Fetus II	Fetus III	Fetus IV	Infant VII	Infant IX	Infant X	Juv. XIII	Juv. XIV	Adult XVII
31 a.	Horiz. head circumf. (m.34) & vertex-coccyx l. (m.1 a) . . . . .	123.8	120.0	128.1	....	....	95.1	....	....	....	....
33 a.	Average head diam. (m.28 a) & Trunk h. (m.4) . . . . .	80.3	80.2	89.8	....	....	....	....	....	40.3	....
34 a.	Head l. (m.30) & sagittal arc of head (m.35) . . . . .	....	56.6	....	....	....	....	....	77.8	....	....
35.	Head br. (m.32) & head l. (m.30) . . . . .	82.8	90.9	82.8	89.2	....	75.6	77.2	78.6	78.9	....
40.	Face br. (m.41) & head br. (m.32) . . . . .	91.7	86.2	102.0	....	....	92.3	....	100.0	98.5	....
43.	Nose br. (m.43) & face br. (m.41) . . . . .	34.1	45.0	38.8	....	....	42.3	....	....	....	....
44.	Nose br. (m.43) & Nose h. (m.42) . . . . .	93.7	133.3	95.1	....	....	78.9	....	....	....	....
45.	Interocular br. (m.44) & biocular br. (m.45) . . . . .	33.3	40.8	35.3	....	....	34.9	....	34.4	....	....
46.	Interocular br. (m.44) & face br. (m.41) . . . . .	27.3	28.4	24.5	....	....	22.7	....	20.0	....	....
47.	Mouth br. (m.46) & face br. (m.41) . . . . .	45.5	45.0	53.1	....	....	53.6	....	55.4	....	....
48.	Ear br. (m.48) & ear h. (m.47) . . . . .	58.4	67.8	62.5	....	....	64.3	....	71.1	....	62.7
49.	Ear h. $\times$ br. (m.47 $\times$ m.48) & Head l. $\times$ tot. h. (m.30 $\times$ m.38) . . . . .	2.3	4.7	4.6	....	....	6.0	....	8.2	....	....
49 a.	Ear h. (m.47) & total head h. (m.38) . . . . .	18.7	26.2	26.7	....	34.7	30.9	....	31.1	....	33.7

<sup>24</sup> Bolk (1926 b) compared the profile of the head of his gorilla fetus with that of a human fetus by superimposing one on the other, without regard to the skull base or the ear-eye horizon, these being situated much higher in the ape than in the human fetus. In this way he reached the following conclusions, which could not have been drawn, if the ear openings of the gorilla had been shifted down to the level of those of the human fetus: "Die starke Gehirnentwicklung [speaking of fetus IV] hat eine Ausbildung der Stirn zur Folge, welche gleich hoch als beim menschlichen Fetus gewölbt ist . . . Diese Superpositionszeichnung zeigt, dass die Schädelwölbung des Gorillafetus mit jener des Menschenfetus ziemlich genau übereinstimmt."

The length-breadth proportion of the head, or the so-called cephalic index (i 35), shows a clear tendency to decrease in general with advancing age, the values for fetal life being higher than those for any of the postnatal growth stages. The marked fluctuations of this index in the fetuses and its apparent slight increase after birth are in all likelihood explained by the great variability in the shape of the head of the gorilla, which ranges from dolichocephaly to brachycephaly, as has been shown by Oppenheim (1912), Bolk (1925), and Harris (1926). That the cephalic index is very high in fetuses of all the higher primates is proved by the following figures: Among many hundreds of human fetuses it averages 87.4 in the third month, decreasing to an average of 81.5 in the ninth month, and ranging individually to as much as 98.0 (Schultz, 1926 b); in gorilla it ranges from 82.8 to 90.9 (Table 7, i 35); in the chimpanzee it varies between 83.1 and 90.7 (the younger fetus of Friedenthal, 1914, has an index of 89.3, the older fetus one of 86.8, Bolk's fetus [1926 b] has the minimum value, and Anthony's fetus [1918] the maximum); in orang-utan variations extend from 78.9 to 95.0 (four fetuses described by Schwalbe [1914], and three fetuses measured by the author, the latter having values of 87.4, 91.7, and 92.1).

The occiput of the head of the gorilla seems to become slightly more prominent with advancing fetal development, since it does not project at all beyond the profile of the neck in fetus I, but is quite prominent in fetus IV. The degree of prominence in the latter specimen is greater than in any other gorilla; particularly in later stages of growth this prominence of the occiput becomes again very much less pronounced, disappearing entirely after infantile life. In man the occiput can be much more prominent than in gorilla fetus IV, at least after the middle of fetal development.

The nose of gorilla becomes in general narrower in relation to its height (i 44) with advancing growth (See Pl. IV, fig. 1 and Pl. VIII, Fig. 1). Fetus II has an extremely broad nose in proportion to nose-height as well as to the breadth of the face (i 43). In fetuses I and II the nasal septum is still very broad, almost as in platyrrhine monkeys, and the nostrils are relatively small. However, in the third known fetal stage of gorilla the septum has already narrowed to the thin partition typical of catarrhines, and the nostrils have become greatly enlarged. Soon after birth the nasal openings of gorilla develop to a proportionate size which exceeds that of any other primate (See Pl. IV, fig. 1 and Pl. VIII, fig. 1). The nose of the two youngest fetuses is, as shown clearly on Pl. VII, at least as prominent as in negro fetuses of corresponding development. The nasal bridge lies far in front of the eyes and there is a distinct nasal apex. In later growth



stages, however, nothing is left of the latter and the nasal bridge has sunk between the bulging eyes in fetuses III and IV. Nevertheless, the gorilla possesses throughout growth a more prominent nose than the other apes, and, indeed, one which is as much elevated as in some human beings. This is best demonstrated by a comparison between the horizontal sections through the nasal region of various higher primates given on Pl. VIII, fig. 2. The interorbital curve *a* of the siamang, orang, and chimpanzee is almost straight, indicating a flat nasal bridge, as in the chimpanzee shown on Pl. IV, fig. 1. The lower curve *b* shows that at their lower end the nasal bones of these apes also do not project forward, but can at times even form a concavity, as in the adult chimpanzee. Man and gorilla form a sharp contrast to these conditions. Section *a* as well as *b* of the juvenile and the adult gorilla are bent forward more strongly than in the flat-nosed negress, but not as much as in the white with an extremely prominent nose. All gorillas after infantile age have, as far as the author can ascertain, along the upper part of the nasal dorsum a median ridge (See Pl. IV, fig. 1) which shows clearly on the horizontal section *a* of the skull.

Just as the nasal aperture lies much further below the lower edge of the orbits in gorilla than in chimpanzee (Pl. VIII, fig. 2) so are the nasal wings further removed from the lower eyelids in the former than in the latter (Pl. IV, fig. 1). In consequence the upper lip of gorilla is much lower than that of chimpanzee or, incidentally, that of orang, differences which are present already in the older fetuses and infants (Pl. VIII, fig. 1). As in all primates, the interocular breadth of gorilla becomes smaller in relation to the face breadth (i 46) with advance in development, but even at the completion of growth the eyes of the gorilla have not approximated one another as much as have the eyes of the orang-utan (See Pl. VIII, fig. 2).

The excessive wrinkling around the eyes, which forms such a characteristic part of the physiognomy of the ape, is already well developed in older fetuses of the anthropoids, whereas in man accessory folds on the eyelids do not as a rule become well marked until old age. In such low races as Hottentots and Bushmen this wrinkling appears earlier, and is more accentuated than in higher races of man.

The relative width of the mouth (i 47) increases with advancing growth in the gorilla, but it is at all times greater than in man (See Pl. III, fig. 2). In regard to the lips of adult gorilla Du Chaillu (1861) states: ". . . the lips are sharply cut, exhibiting no red on the edges, as in the human face." It is very interesting to find that this difference between gorilla and man is not yet present in fetal life, since the gorilla fetuses II, III, and IV have lips at least as broad as negro fetuses and even in gorilla infants is the mucous membrane of the lower lip still

visible on the closed mouth (Pl. VII, Pl. VIII, fig. 1; and Pl. IV, fig. 1). However, there exists a difference between gorilla and human races in regard to the conditions of growth of the lips. In gorilla the lips change during development from very broad to extremely narrow, but in man they do not change, since they are either broad in fetuses and in adults, as in negroes, or narrow in early and late stages of growth, as in whites. In view of the fact that Klaatsch (1912) has expressed the opinion that the total absence of a philtrum in apes represents phylogenetically a secondary condition, it is important to state that none of the fetuses of apes showed any trace of a philtrum, nor incidentally of a tuberculum labii superioris, features which are strongly developed in man. This, of course, does not necessarily contradict Klaatsch's theory, though one might have expected indications of these structures at some prenatal stage of the apes.

There remains to be discussed in this chapter the growth of the ear. The height-breadth proportion (i 48) of the gorilla's ear varies between 58 and 71 without showing any definite growth change. The two indices (i 49 & i 49a) expressing the relative size of the ear increase greatly with advancing development. It may be said, therefore, that the ear of gorilla becomes steadily larger in proportion to the size of the head. In this respect the gorilla agrees with the chimpanzee but differs from man and the orang, in which the relative size of the ear increases at first, but decreases again in postnatal life, as has been shown by the writer in

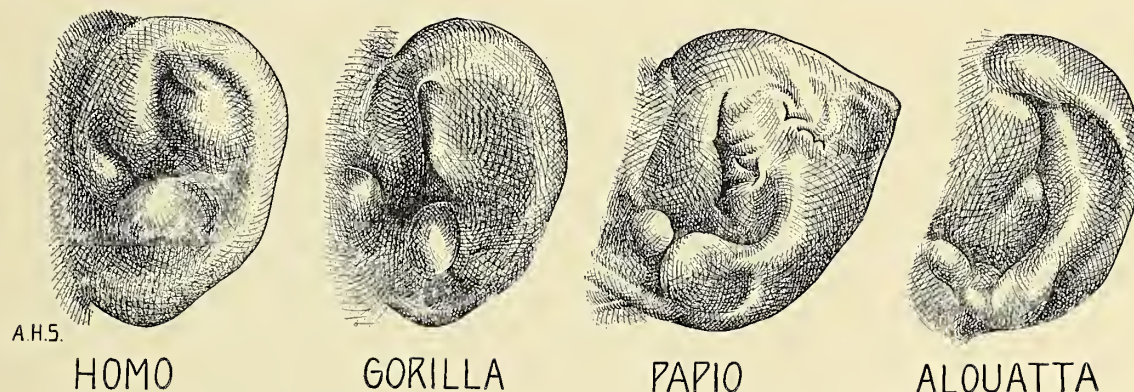


Fig. 2. Outer ears of human fetus, gorilla fetus II, baboon fetus (*Papio papio*), and howler-monkey fetus (*Alouatta palliata*); all corresponding in development to about the fifteenth week in man.

previous papers (1925 & 1926 a). The ear of the gorilla is larger than the ear of the orang, but in general smaller than the ear of the chimpanzee. Individually, however, there occur such marked variations in the size of the ear of the latter two apes, that the difference may occasionally disappear, as has been shown by Matschie (1919) and others.



The helix of gorilla fetus II is not yet rolled in. In fetus III the upper third of the edge of the helix is folded over, in fetus IV two thirds, and in the infant shown on Pl. VII the entire margin of the ear is bent in. No trace of a Darwinian tubercle can be recognized on any of the fetal or infantile ears of gorillas, though Hartmann (1880) states that it occurs occasionally in the gorilla. A glance at text figure 2 is convincing proof that the fetal ears of gorilla and man differ far less from one another than from the fetal ears of catarrhine or platyrrhine monkeys. A marked difference between the former two consists in the wide separation between tragus and antitragus in the gorilla and the close approximation of these structures in man. This distinction, however, is not constant, since in gorilla fetus III and IV tragus and antitragus almost touch one another, and in some few human ears the author found them to be as widely separated as in fetus II. Finally, attention is called to the fact that all the fetuses of gorillas possess a well developed lobule. In older gorillas such a free lobule of the ear is also frequently present (*e.g.* in the adult XVII of Ehlers, 1881) but in many cases it may be missing (Hartmann, 1880), as also may happen in man.

### PART III.

#### Chapter 11. THE BODY PROPORTIONS OF HIGHER PRIMATES IN FETAL AND ADULT LIFE.

Every part of the body is represented by the proportions listed in Table 8. A comparison between the various primates, based upon these relative measurements, can reasonably be expected to impartially take into consideration all their different specializations as well as similarities. For such a comparison it is very essential to bear in mind that all body proportions vary individually to a very considerable extent. This fact is shown, for instance, by the wide ranges of variations in the proportions of the small series of human fetuses and adults, as given in Table 8. Of the apes each type and age is represented in the table by only one specimen, the proportions of which may not be typical for the particular species and stage of development. For these reasons only marked differences between the proportions of different individual apes can be regarded as significant. Generally speaking, a difference can be relied upon as being "marked" and really significant, if it surpasses in amount the range of variation of the given proportion in a series of individuals of one of two kinds of primates compared.

TABLE 8.

The body proportions of higher primates in fetal life (at stages of development corresponding to that of gorilla fetus II) and in adult life. In the series of man the minimum, maximum, and average values are given. The indices for adult gorilla marked with \* are those of specimen XVI.

Index No.	Percentage relation between:	FETUSES							ADULTS						
		Man (series 1)			Gorilla	Chmp.	Orang.	Gib'n	Man (series 5)			Gorilla	Chmp.	Orang.	Gib'n
		Min.	Max.	Aver.	II	2.	3.	4.	Min.	Max.	Aver.	XVII	6.	7.	8.
1.	Chest circumf. (m.14) & trunk h. (m.4)	184.5	229.5	206.1	231.5	....	....	198.2	146.6	194.3	168.3	180.0*	....	157.3	167.8
2.	Shoulder br. (m.9) & trunk h. (m.4)	57.9	77.8	66.7	72.9	80.7	....	58.4	59.4	81.0	67.6	60.8	72.0	44.7	68.0
3.	Hip br. (m.10) & trunk h. (m.4)	43.9	54.3	48.9	46.3	42.4	....	39.0	54.6	68.6	61.5	....	57.0	47.7	48.8
4.	Hip br. (m.10) & shoulder br. (m.9)	64.3	86.4	73.7	63.5	52.6	....	66.9	81.3	102.3	91.2	....	79.1	106.8	71.7
5.	Trans.chest diam. (m.12) & sag. chest diam. (m.13)	113.0	133.3	120.5	109.0	....	....	111.7	120.0	154.0	130.5	....	....	114.7	117.7
6.	Shoulder h. (m.6) & trunk h. (m.4)	2.6	16.2	7.3	19.2	....	....	6.3	-0.8	+2.3	+0.1	....	....	18.8	11.2
7.	Nipple br. (m.11) & trans. chest diam. (m.12)	50.0	68.0	58.1	57.9	....	....	47.0	61.3	80.6	71.5	....	....	69.3	25.8
8.	Nipple h. (m.7) & trunk h. (m.4)	73.0	85.3	77.6	83.7	....	....	81.6	66.9	78.3	73.9	....	....	89.9	87.3
9.	Umbilicus h. (m.8) & trunk h. (m.4)	11.4	22.9	17.2	20.9	....	....	15.3	23.5	36.7	29.8	17.8	....	21.6	30.4
10.	Total upper limb l. (m.22) & trunk h. (m.4)	113.6	145.6	132.7	163.2	157.4	....	181.5	128.1	166.0	144.8	156.0	170.0	207.2	280.0
11.	Upper arm + forearm l. (m.23 + 24) & sitting h. (m.1)	40.3	47.7	43.8	52.3	50.4	74.0	71.4	61.3	70.0	64.5	....	....	81.6	105.4
12.	Upper arm l. (m.23) & total upp. limb l. (m.22)	41.6	45.5	43.6	37.7	33.5	35.8	38.5	38.5	44.9	40.7	40.6	36.5	35.6	34.6
13.	Forearm l. (m.24) & total upper limb l. (m.22)	31.2	34.0	32.7	32.1	32.9	37.4	34.9	30.8	36.1	33.9	33.6	34.0	36.0	36.9
14.	Hand l. (m.25) & total upper limb l. (m.22)	20.7	25.5	23.7	30.2	33.6	26.8	26.6	24.3	26.3	25.4	25.8	29.5	28.4	28.5
15.	Forearm l. (m.24) & upper arm l. (m.23)	69.1	80.9	75.2	85.2	98.2	104.6	90.5	76.2	92.4	83.6	82.9	93.4	101.0	106.6
16.	Hand l. (m.25) & forearm l. (m.24)	61.1	81.2	72.3	93.9	101.7	71.7	76.3	68.4	78.9	74.9	76.5	86.4	78.9	77.5
17.	Thumb l. (m.26) & hand l. (m.25)	64.0	77.3	73.0	48.0	....	....	56.5	65.1	74.3	69.2	42.7*	....	46.1	49.0
18.	Hand br. (m.27) & hand l. (m.25)	48.0	61.8	54.3	39.0	....	....	34.5	42.1	52.2	45.4	36.6*	....	30.6	23.5
19.	Total lower limb l. (m.15) & trunk h. (m.4)	105.1	132.8	116.7	107.9	106.5	....	104.6	160.8	198.5	175.4	110.8	113.7	130.1	169.5
20.	Thigh + leg l. (m.16 + 18) & sitting h. (m.1)	41.8	49.4	46.4	45.6	46.8	59.9	54.1	90.9	107.5	97.2	....	....	66.0	84.8
21.	Leg l. (m.18) & thigh l. (m.16)	65.2	84.1	75.7	78.8	90.7	103.8	77.2	74.4	91.1	84.1	88.4	90.7	89.2	91.4
22.	Foot l. (m.19) & leg l. (m.18)	71.1	95.0	81.5	106.7	98.0	98.1	92.5	65.0	73.0	68.7	97.6	102.0	118.8	91.7
23.	Foot l. (m.19) & sitting h. (m.1)	14.7	18.0	16.2	21.5	21.8	29.9	21.8	29.0	32.8	30.5	....	....	36.9	37.1
24.	Foot br. (m.21) & foot l. (m.19)	27.6	34.2	30.6	31.6	....	....	26.2	24.3	31.6	28.0	....	....	23.8	21.6
25.	Great toe l. (m.20) & foot l. (m.19)	92.7	100.0	95.9	89.0	....	....	88.6	97.3	102.4	99.8	....	....	55.9	84.1
26.	Total upper limb l. (m.22) & total lower limb l. (m.15)	108.0	120.4	113.8	151.2	147.7	....	173.4	78.7	87.6	82.5	140.7	149.2	159.2	165.0
27.	Upper arm + forearm (m.23 + 24) & thigh + leg (m.16 + 18)	87.5	102.7	94.6	114.5	107.7	123.5	131.9	63.1	71.5	66.4	115.8	116.4	123.7	124.3
28.	Upper arm l. (m.23) & thigh l. (m.16)	86.4	104.5	94.9	110.6	103.6	123.0	122.7	60.4	74.2	66.6	119.2	114.8	116.4	115.3
29.	Forearm l. (m.24) & leg l. (m.18)	88.9	107.1	94.4	119.6	112.2	124.0	143.8	57.9	71.9	66.1	111.9	118.2	131.8	134.4
30.	Hand l. (m.25) & foot l. (m.19)	73.3	96.3	83.9	105.2	116.6	90.6	118.8	68.4	77.2	72.0	80.4	100.0	87.6	113.7
31.	Aver. head circumf. (m.29) & sitting h. (m.1)	107.3	122.3	114.2	109.3	....	....	100.4	56.9	65.6	61.6	....	....	60.7	86.1
32.	Aver. head diam. (m.28 a) & sitting h. (m.1)	32.9	38.5	35.5	36.8	32.3	38.4	35.1	18.2	21.0	19.7	....	....	21.0	28.9
33.	Aver. head diam. (m.28) & trunk h. (m.4)	67.4	89.5	77.6	72.4	59.8	....	61.3	27.9	34.0	31.1	....	28.5	34.8	48.0
34.	Nasion—inion l. (m.31) & sagittal arc (m.35)	36.5	47.2	42.0	54.7	....	....	56.4	45.3	51.6	48.5	....	....	63.5	61.6
35.	Head br. (m.32) & head l. (m.30)	76.5	94.3	87.6	90.9	89.3	94.3	89.0	71.4	86.9	79.3	....	74.3	88.2	85.1
36.	Head h. (m.33) & head l. (m.30)	74.3	85.3	78.4	68.0	64.0	....	76.0	69.0	79.4	73.8	....	45.1	68.8	58.1
37.	Total face h. (m.39) & trunk h. (m.4)	30.8	41.4	35.7	40.4	35.9	....	28.3	20.5	26.1	23.2	....	25.0	34.8	31.2
38.	Upper face h. (m.40) & aver. head circumf. (m.29)	7.8	10.2	9.0	13.1	....	....	11.0	12.5	16.0	14.2	....	....	24.1	13.5
39.	Total face h. (m.39) & head h. (m.33)	45.6	62.5	52.3	70.7	79.1	....	53.8	77.2	94.3	85.4	....	142.2	124.5	90.7
40.	Face br. (m.41) & head br. (m.32)	80.0	89.7	84.3	86.2	....	....	84.3	75.2	95.8	90.4	....	....	100.7	86.5
41.	Upper face h. (m.40) & face br. (m.41)	30.8	41.7	37.0	47.6	....	....	39.7	46.8	63.7	55.8	....	....	74.0	50.5
42.	Nose h. (m.42) & upper face h. (m.40)	60.0	77.8	67.9	70.8	....	....	82.3	63.4	75.0	71.3	....	....	58.1	80.0
43.	Nose br. (m.43) & face br. (m.41)	20.8	28.3	25.4	45.0	....	....	20.5	22.7	26.8	24.6	....	....	27.5	19.3
44.	Nose br. (m.43) & Nose h. (m.42)	85.7	116.7	102.0	133.3	....	....	62.7	52.5	70.8	62.1	....	....	63.9	47.8
45.	Interocular br. (m.44) & Biocular br. (m.45)	40.4	50.0	45.5	40.8	....	....	40.7	29.4	38.7	33.1	....	....	26.9	29.0
46.	Interocular br. (m.44) & face br. (m.41)	29.6	37.5	34.3	28.4	....	....	33.9	19.1	27.5	23.0	....	....	14.8	20.7
47.	Mouth br. (m.46) & face br. (m.41)	30.7	39.1	34.7	45.0	....	....	52.5	31.2	41.9	35.8	....	....	54.9	53.2
48.	Ear br. (m.48) & ear h. (m.47)	50.0	71.4	59.7	67.8	....	....	81.4	44.6	58.6	51.0	62.7	....	66.7	77.8
49.	Ear h. × br. (m.47 × 48) & head l. × tot. h. (m.30 × 38)	1.8	3.0	2.5	4.7	....	....	3.8	3.9	5.8	4.7	....	....	2.5	10.0

NOTE—l.=length; br.=breadth; h.=height; trans.=transverse.



Based upon such considerations Mollison (1908) has introduced a very useful mathematical method by which it is possible to express the degree of similarity between different races or species in relation to the variability of the characters under investigation. This method is best explained by the following concrete examples. The relative length of the upper limb (i 10, Table 8) amounts to 156.0 in the adult gorilla and, on an average to 144.8 in adult man, *i.e.*, there exists a difference of 11.2 index units between the two values, which represents the absolute deviation of the one from the other. Individually this same proportion ranges in man to a maximum of 166.0, or to 21.2 index units above the average value in man. Since the value of gorilla lies above the average value in man, only the range of variation in the latter above the average ("positive range") is of interest in this case. The absolute deviation of 11.2 is now expressed in percentage of this positive range of variation in man (21.2) so that a *relative* deviation is obtained, which in this instance amounts to + 52.8. The latter figure shows clearly and precisely that the particular gorilla stands in regard to its relative upper limb-length half way between the average and maximum of this proportion in man, and that therefore these two primates do not differ significantly in regard to this character. On the other hand, the adult gibbon has a relative upper limb length of 280.0, or a value deviating from the average in man for 135.2 index units. This absolute difference amounts to 637.7 per cent of the positive range in man. Judging by the latter deviation index the gibbon differs very markedly from man in relative limb-length, indeed more than six times as much as the average differs from the maximum value in man (= 100) and more than three times as much as the minimum human variation differs from the maximum (= 200).

The deviation index can be expressed by the following formulæ:  $+ di = \frac{x - A}{ma - A} \times 100$ , in case the particular proportion to be compared lies above the average proportion of the series which serves as a basis for the comparison; or  $- di = \frac{A - x}{A - mi} \times 100$ , in case the value to be compared is smaller than the average of the series. In these formulæ *di* stands for deviation index (+ or — merely indicating the direction of the deviation from the average), *x* for the value of a given proportion in the specimen to be compared, *A* for the average of the same proportion in the series used as basis for the comparison, and *ma* and *mi* for the maximum and the minimum values of the same proportion in the same series.

The deviation indices for a number of characters can be used for the construction of deviation curves, as has been done in text-figures 3 and 4. For this purpose all the averages of the series are placed at equal distances on a straight line. At arbitrary, but equal, distances on either side are drawn two lines parallel

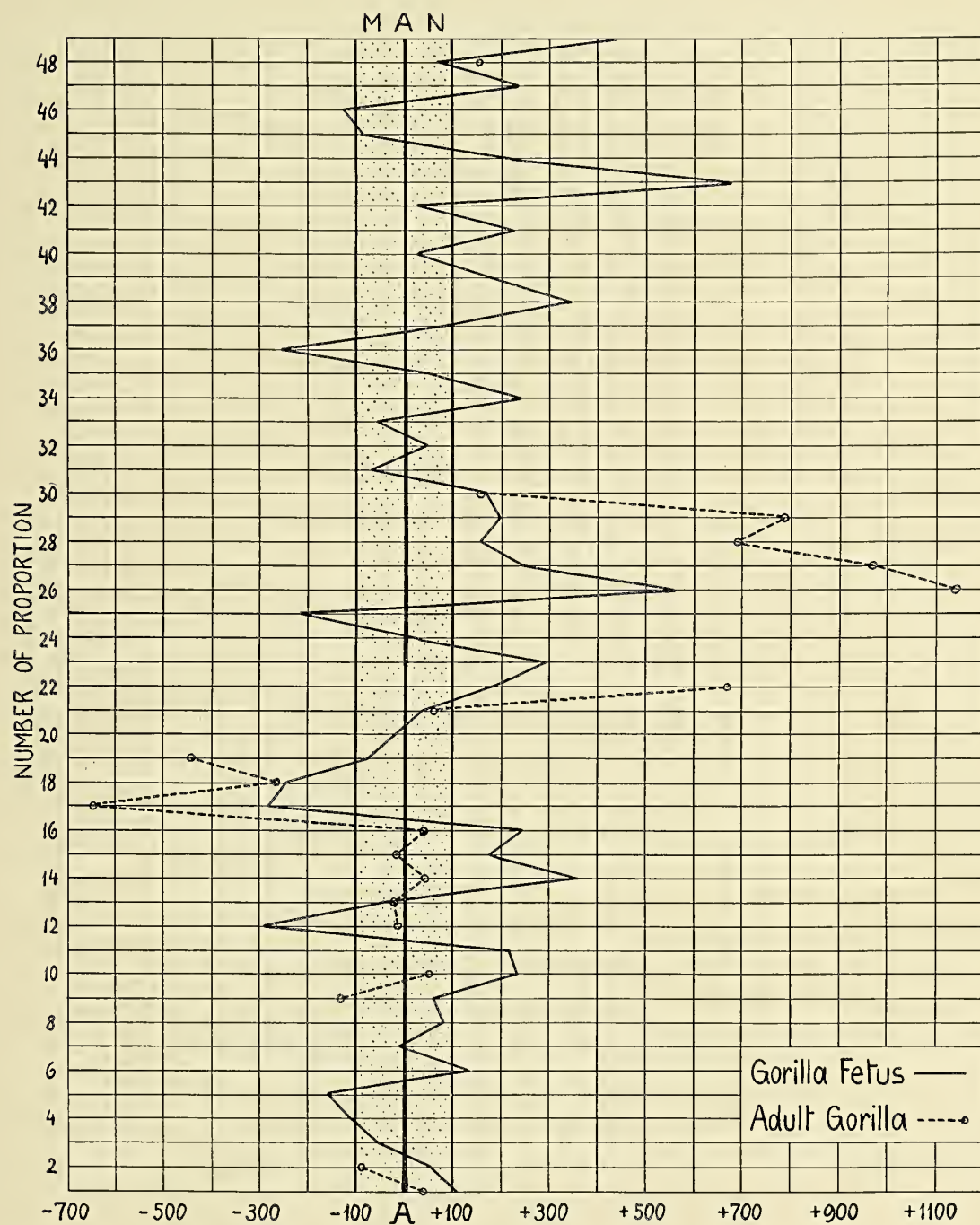


Fig. 3. Deviation curves (constructed from deviation indices in Table 9) of the proportions of gorilla fetus II and of adult gorilla XVII. The forty-nine proportions are arranged in the same sequence as they are listed in Table 8, *i.e.*, the proportion numbers, given on the left margin of this figure, correspond to the index numbers in Tables 8 and 9. The dotted area between -100 and +100 and the heavy line A represent the range of variation and the average of the proportions of human fetuses (Series 1) as well as those of human adults (Series 5), since the bases of the two curves have been superimposed on one another.



to the line of averages. These two new lines represent, and inclose between them, the ranges of variation of all the proportions of the series; their distance from the middle line is given the value of 100, which thus furnishes the scale for the plotting of the deviation curves. A curve, which would move entirely within the ribbon enclosed by the  $-100$  and  $+100$  lines, would constitute a reliable proof for the assumption that the specimen from which the curve was derived does not differ from the series used as a basis for comparison. On the other hand, should all the points of construction of a curve fall outside the lines marked 100, the specimen in question would differ in every character examined from the individuals of the series. Naturally, this difference would be the greater, the further the curve is removed from the base line  $A$ . It will now be understood that this method is capable of establishing and illustrating the exact relative degree of similarity between different animals in regard to their measurable characters. Furthermore, with these indices and their combination in the form of curves, it is possible to analyze the general degrees of similarity by finding readily which particular characters differ most and which others least. For instance, twenty proportions, for which data are available in both a gorilla fetus and an adult gorilla, have an average deviation index of 190.7 in the former but in the latter one of 320.5. The fetus, therefore, is in general less different from human fetuses than the adult is different from human adults. Of the various proportions, however, some show a much greater difference in degree of similarity than do others, as demonstrated by text-figure 3 (See also Table 9). Thus it is found that the proportion between the lengths of thigh and leg (i 21) has a deviation index of 36.9 in the gorilla fetus and one of 61.4 in the adult gorilla. This character, therefore, does not differ appreciably from its condition in man in fetal as well as in adult life. In contrast to this the proportion between the lengths of forearm and leg (i 29) has a deviation index in the fetus of 198.4 and in the adult of 790.0, or one nearly four times as large as the fetal value. Text-figure 3 shows also that in nineteen out of the forty-nine characters considered the fetus of the gorilla falls within the range of variation in human fetuses, and in only nineteen other characters does it differ from the human average more than the human minimum variation differs from the maximum variation, *i.e.*, it has deviation indices above 200.

In text-figure 4 the deviation curves of the various primate fetuses are compared with each other. A study of these curves leads to three general conclusions of considerable importance. First of all, it can be seen at a glance that by and large all the curves maintain a surprisingly similar course. In other words, in the great majority of characters all the fetuses of apes deviate from the human fetal

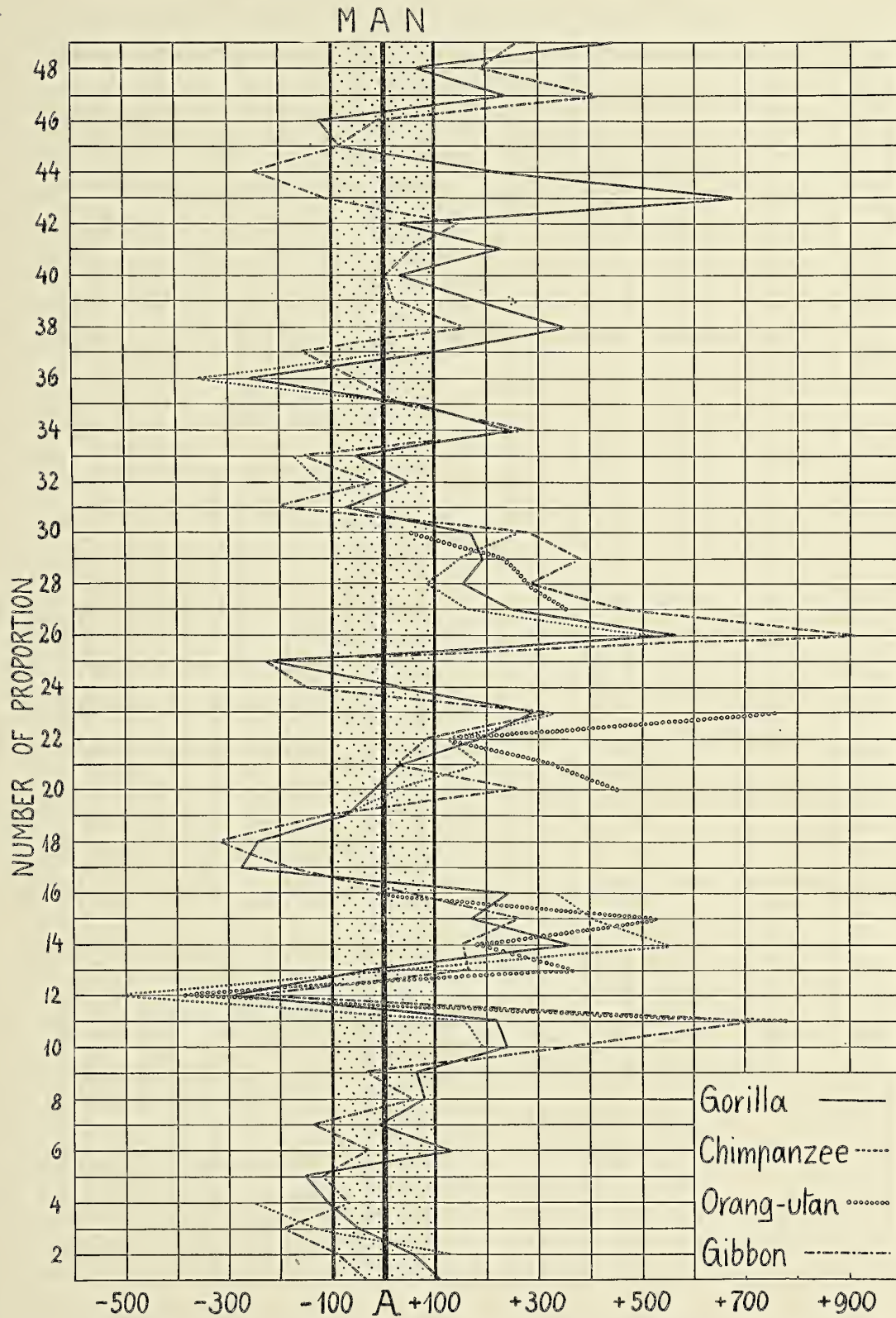


Fig. 4. Deviation curves of the proportions of the ape fetuses in Table 8. The dotted area represents the range of variation, and the heavy line A the average of the proportions in Series 1 of human fetuses.



condition in corresponding directions, *i.e.*, either all to the right or all to the left. This must be interpreted as indicating, that in regard to most proportions, man represents one extreme among the higher primates, the opposite extreme being formed by one or another of the apes. In other words, the human proportions fall rarely within the range of different values of the same characters among the apes. These statements, however, do not imply that man is in most respects further removed from the apes than are some apes from others. Many examples could be mentioned to show that there exist much greater gaps between one ape and another ape than between man and some ape. To quote just two instances in support of this last assertion: The proportion between the lengths of forearm and upper arm (i 15) has a deviation index in the fetus of the gorilla of only + 175.3, but in the fetus of the orang-utan one of + 516.0; the deviation index for the relative foot-length (i 23) amounts in the fetus of the gorilla to + 294.2 but in the fetus of the orang-utan to + 761.5. In regard to both these proportions man and gorilla differ very much less than do the gorilla and the orang.

The second conclusion based upon text-figure 4 consists in the interesting fact that by far the most marked deviations of the curves are found in the proportions of the limbs (i 10 to i 30) and the smallest deviations in those of the trunk (i 1 to i 9), whereas the proportions of the head (i 31 to i 49) occupy in general an intermediate position in this respect. It can be stated, therefore, that the various diverging evolutionary specializations of the higher primates must have affected the limbs much more than the trunk.

Finally, as a third conclusion it may be mentioned that in general the fetus of the gorilla deviates to a lesser degree from human conditions than do the fetuses of the other apes. Of this more will be said later on.

TABLE 9.  
Deviation indices of the body proportions of the fetal and adult primates listed in Table 8.

Index No.	FETUSES				ADULTS			
	Gorilla II.	Chimpanzee 2	Orang 3	Gibbon 4	Gorilla XVII	Chimpanzee 6	Orang 7	Gibbon 8
1.	+108.5	.....	.....	- 36.5	+ 45.0	.....	- 50.7	- 2.3
2.	+ 55.8	+126.1	.....	- 94.3	- 82.9	+ 32.8	-279.3	+ 3.0
3.	- 52.0	-130.0	.....	-197.8	.....	- 65.2	-200.0	-198.5
4.	-108.5	-224.6	.....	- 72.4	.....	-122.3	+140.5	-197.0
5.	-153.3	.....	.....	-117.2	.....	.....	-150.3	-121.9
6.	+133.7	.....	.....	- 21.2	.....	.....	+850.3	+505.0
7.	- 2.5	.....	.....	-137.0	.....	.....	- 21.6	-448.0
8.	+ 79.2	.....	.....	+ 51.9	.....	.....	+363.5	+304.5
9.	+ 64.9	.....	.....	- 32.8	-126.9	.....	-130.0	+ 8.7
10.	+236.2	+191.4	.....	+378.1	+ 52.8	+118.8	+294.3	+637.7
11.	+217.8	+169.1	+774.5	+708.0	.....	.....	+311.0	+744.0
12.	-295.0	-505.0	-390.0	-255.0	- 4.5	-190.8	-232.0	-277.2

Index No.	F E T U S E S				A D U L T S			
	Gorilla II.	Chimpanzee 2	Orang 3	Gibbon 4	Gorilla XVII	Chimpanzee 6	Orang 7	Gibbon 8
13.	- 39.9	+ 15.4	+361.5	+169.1	- 9.7	+ 4.5	+ 95.5	+136.3
14.	+361.0	+550.0	+172.1	+161.0	+ 44.4	+455.5	+333.3	+344.5
15.	+175.3	+403.3	+516.0	+268.0	- 9.5	+111.2	+197.8	+261.3
16.	+242.7	+330.2	- 5.4	+ 44.9	+ 40.0	+287.5	+100.0	+ 65.0
17.	-277.8	.....	.....	-183.3	-646.0	.....	-563.5	-492.5
18.	-242.8	.....	.....	-314.2	-266.3	.....	-448.7	-664.0
19.	- 75.8	- 88.0	.....	-104.2	-442.3	-422.3	-310.0	- 40.4
20.	- 17.4	+ 13.3	+450.0	+256.4	.....	.....	-495.0	-196.9
21.	+ 36.9	+178.5	+334.5	+ 17.9	+ 61.4	+ 94.3	+ 72.9	+104.2
22.	+186.6	+122.2	+123.0	+ 81.6	+672.0	+774.7	+1164.0	+535.0
23.	+294.2	+311.0	+761.5	+311.0	.....	.....	+234.7	+286.9
24.	+ 27.8	.....	.....	-146.5	.....	.....	-113.5	-172.8
25.	-215.5	.....	.....	-228.0	.....	.....	-1755.0	-628.0
26.	+566.6	+514.0	.....	+903.0	+1140.0	+1307.0	+1504.0	+1616.0
27.	+245.5	+161.8	+356.8	+460.5	+969.0	+980.0	+1123.0	+1134.0
28.	+163.6	+ 90.6	+292.9	+289.7	+692.0	+634.0	+655.0	+640.6
29.	+198.4	+140.2	+233.0	+389.0	+790.0	+898.0	+1132.0	+1176.0
30.	+171.7	+263.8	+ 54.0	+281.4	+161.3	+538.5	+300.0	+802.0
31.	- 71.0	.....	.....	-200.0	.....	.....	- 19.2	+612.8
32.	+ 43.3	-123.0	+ 96.7	- 15.4	.....	.....	+100.0	+707.0
33.	- 51.0	-174.5	.....	-159.8	.....	- 81.2	+127.5	+583.0
34.	+244.2	.....	.....	+277.0	.....	.....	+484.0	+423.0
35.	+ 49.2	+ 25.4	+100.0	+ 29.0	.....	- 63.3	+117.0	+ 76.3
36.	-253.6	-351.2	.....	- 58.5	.....	-597.7	-104.1	-327.0
37.	+ 82.4	+ 3.5	.....	-150.8	.....	+ 62.1	+400.0	+275.7
38.	+341.2	.....	.....	+166.7	.....	.....	+550.0	- 41.2
39.	+180.3	+262.8	.....	+ 14.7	.....	+638.2	+439.5	+ 59.5
40.	+ 35.2	.....	.....	0	.....	.....	+190.8	- 25.6
41.	+225.6	.....	.....	+ 57.5	.....	.....	+230.5	- 58.9
42.	+ 29.3	.....	.....	+145.4	.....	.....	-167.0	+235.0
43.	+676.0	.....	.....	-106.4	.....	.....	+131.8	-278.9
44.	+212.8	.....	.....	-241.0	.....	.....	+ 20.7	-149.0
45.	- 92.1	.....	.....	- 94.1	.....	.....	-167.5	-110.7
46.	-125.4	.....	.....	- 8.5	.....	.....	-210.5	- 59.1
47.	+234.1	.....	.....	+404.5	.....	.....	+313.0	+287.0
48.	+ 69.2	.....	.....	+185.5	+154.0	.....	+206.5	+352.7
49.	+440.0	.....	.....	+260.0	.....	.....	-275.0	+482.0
AVER.	173.5	210.3	313.9	189.5	320.5	385.5	364.8	365.1

The deviation indices of all the proportions contained in Table 8 are listed in Table 9. By figuring averages from these indices it is possible to compare the relative degrees of similarity of the different primates in a condensed and clear manner. Such averages, however, can as yet be only preliminary and tentative, inasmuch as data for many proportions in several of the apes are still wanting. For the same reason it was necessary to calculate more than one average from each column in Table 9. It must also be mentioned that the absolute size of these averages is naturally meaningless in itself, since it is dependent entirely on the



number of characters upon which it is based.<sup>25</sup> However, such average deviation indices, as are derived from the same proportions in different apes, are of considerable value for comparisons, since they furnish an impersonal scale for the evaluation of the *relative* amount of difference between the various higher primates. In general these averages become the more reliable and representative, the greater the number of characters considered.

An attempt is made first of all to answer by means of these averages the question whether the apes are less removed from man in fetal than in adult life. The following data are available for this purpose.

Average deviation indices based upon the greatest number of proportions which are known in both the fetus and the adult of a given ape:

Gorilla (twenty proportions): fetus 190.7; adult 320.5.

Chimpanzee (twenty-two proportions): fetus 220.6; adult 385.5.

Orang-utan (sixteen proportions): fetus 313.9; adult 416.5.

Gibbon (forty-nine proportions): fetus 189.5; adult 365.1.

In the gibbon, the only ape in which all forty-nine proportions are available for fetus and adult, the maximum deviation index equals 903 in the fetus and in the adult 1616. In the former 35 per cent of all the proportions have deviation indices above 200 whereas in the latter this percentage has increased to 59.

All these figures demonstrate very clearly and without any exception, that in regard to their body proportions the fetal apes are much more similar to human fetuses than are the adult apes to adult men. This is also evident from the data collected in Table 10, which, however, are based upon a smaller number of proportions (all appertaining to the limbs). The figures in this table refer in every case to the same proportions, so that they permit not only a comparison between the values for fetal and adult life in one and the same ape, but also one between the values of the different apes. The average deviation indices in Table 10, just as the above listed averages, are much larger in the adults than in the fetuses (See also text-figure 5). The maximum deviation indices, likewise, attain much higher values in the former than in the latter. These figures, furthermore, show that the differences between the degrees of deviation of the various apes from man are not yet as marked in fetal as in adult life. The average deviation indices range in the fetuses only between 192 and 258, but in the adults from 314 to 498. This greater

<sup>25</sup> These averages are furthermore influenced by the extent of the range of variation in the series, which serves as a basis for comparison. For instance, the average range of variation of all the proportions amounts in the series of human fetuses to 14.6, but in the series of human adults to only 12.9. Theoretically it could be expected, therefore, that, if the series of adults had a range of variation equal to that of the series of fetuses, the deviation indices of the adult apes would be reduced for 11.6 per cent of their actual amounts.

uniformity in the relative deviations of the fetuses than in that of the adults is graphically shown by the concentric semi-circles of the diagram in text-figure 5.

No alternative seems possible in the interpretation of these findings. The

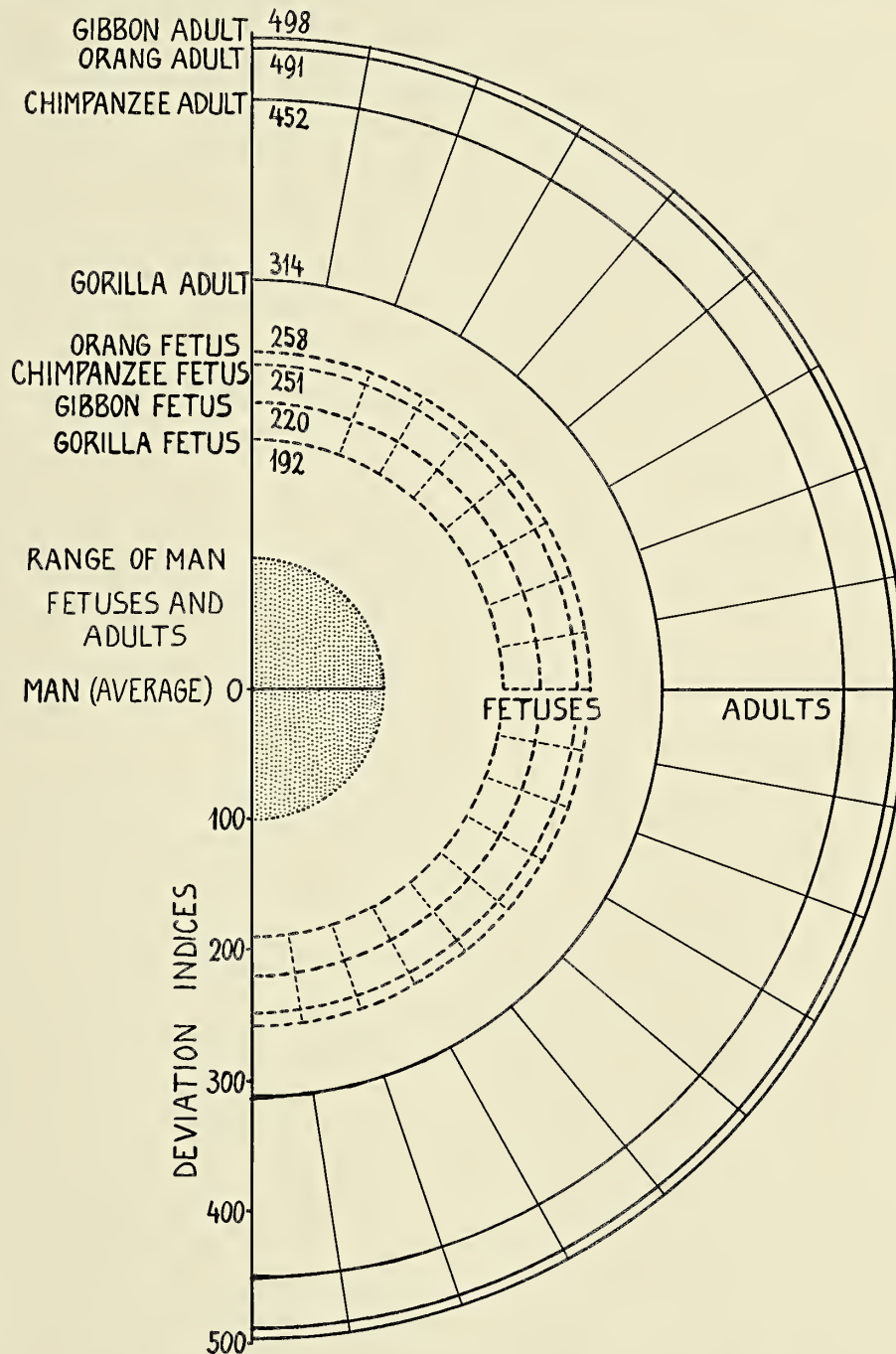


Fig. 5. Diagrammatic representation of the average deviation indices, listed in Table 10. These averages form the radii of the concentric semi-circles. Note that all the adult apes are further removed from man than are any of the fetal apes and that the circles for the fetuses are closer together than those for the adults.



higher primates are more closely alike in early than in later stages of growth, since they all inherited the same developmental process from one common ancestral stock, a process which could have become altered only after their separation into diverging branches. Just as the various specializations became more and more accentuated with advancing evolution of the species, so do the differences between the different primates become in general more and more marked with advance in individual development. Similar statements have been made many times before, but these had always been based upon impressions alone. The correctness of the latter is now proved by means of figures. Thus it can be said that the age-changes in the average and maximum deviation indices constitute a new support for an old hypothesis, namely for the recapitulation theory. These age-changes show nothing more nor less than that the increasing phylogenetic specializations are in general repeated and paralleled by increasing ontogenetic differentiations. These conditions could not be understood and explained without the assumption of one origin for all the higher primates.

TABLE 10.  
Deviation indices of the eleven body proportions which are available in  
all the fetal and adult primates listed in Table 8.

		Average Deviation index	Maximum Deviation index	Percentage of Deviation indices above 200
Gorilla	fetus	192.4	361.0	36.4
	adult	314.0	969.0	36.4
Chimpanzee	fetus	251.0	550.0	45.5
	adult	451.7	980.0	63.6
Orang-utan	fetus	258.1	516.0	63.6
	adult	491.4	1164.0	63.6
Gibbon	fetus	219.9	460.5	54.5
	adult	497.8	1176.0	72.7

Another deduction, reached from the figures in Table 10 and their diagrammatic representation in text-figure 5, carries the last conclusion a step further, inasmuch as it indicates the proportionate degrees of separation which the various primates have reached in the course of their divergent evolution from a common source. All the data agree in the fact that gorilla possesses in fetal as well as in

adult life the lowest deviation indices of all apes. The gibbon, curiously enough, ranks next in the fetal stage, but at the completion of growth it has not only the highest average and maximum deviation indices among all the apes, but also the greatest percentage of indices above 200. If a greater number of proportions than that used in Table 10 is considered, the relative degrees of similarity of the various apes do not change materially in adult life, but among the fetuses the gibbon is shifted from second to third place. These new and somewhat more representative values are given below.

Average deviation indices of adult apes, based upon the fifteen proportions which are available in all adults:

Gorilla	Chimpanzee	Gibbon	Orang-utan
304.5	456.7	518.2	519.5

Again it is the gorilla, which according to these figures stands nearest to man, whereas the orang-utan and the gibbon, with practically the same averages, show the greatest differences from human conditions. The chimpanzee, which in this respect occupies an intermediate position, is by the above average somewhat further removed from the Asiatic apes than it is by its average in Table 10.

Average deviation indices of ape fetuses based upon the sixteen proportions available in the orang-utan fetus:

Gorilla	Chimpanzee	Gibbon	Orang-utan
171.2	212.7	233.6	313.9

Average deviation indices of ape fetuses, based upon the twenty-six proportions available in the chimpanzee fetus (leaving out the orang-utan fetus):

Gorilla	Chimpanzee	Gibbon
169.3	210.3	225.8

The twenty-six body proportions, which have been used for the last figures, differ on an average between the gorilla fetus and the average human fetus for 169 per cent of the difference between the average and maximum values of these proportions in man. This means that the particular gorilla stands in regard to these twenty-six characters closer to the most extreme human variation than the latter stands to the human average.<sup>26</sup> If the difference between extreme and average equals 100, then that between gorilla and human extreme amounts to only 69. The difference between the gorilla and the gibbon fetus is on the same scale 57 (226 minus 169). Based upon these simple calculations it can be stated that there

<sup>26</sup> To find an individual which possesses in every one of the proportions the extreme variation thereof is, of course, as improbable as it is that there should exist some other individual representing a combination of the average conditions of all proportions. With these facts in mind it is readily understood that the above generalizing deductions can have only a theoretical value.



exists nearly as small a difference between a gorilla fetus and the most extreme human fetus as between the former and a gibbon fetus.

It can hardly be regarded as a mere chance occurrence that the greatest average deviation indices are found in the exclusively arboreal apes, the gibbon and orang-utan, whereas the lowest index coincides with the least arboreal type, the gorilla. It can be predicted without any risk, that, if a series of oranges or of gibbons should ever be used as a basis for deviation indices in the other higher primates, the most terrestrial form, man, would show the highest indices and the largely terrestrial gorilla the second highest.

It remains to consider in a brief and preliminary way the important problem whether the various primates differ in regard to the relative amount of ontogenetic change in their body proportions. This question can be answered by means of the following method applied to the figures in Table 8. If the difference between the values of a proportion in fetal and in adult life is calculated in percentage of the value of this proportion in the fetus, an index is obtained which expresses the relative amount of ontogenetic change in this proportion. It was shown by the author in a previous paper (1926 b) that the degrees of developmental change vary widely in different proportions, *i.e.*, whereas some proportions may remain almost unaltered throughout growth, others may change very profoundly. For generalizing statements it is essential, therefore, to figure averages from the relative amounts of ontogenetic change in the various proportions.<sup>27</sup> From all the forty-nine proportions such averages can be formed only in man and in the gibbon. In the former it is found to amount to 32.2 and in the latter to 24.8. This means that on an average the forty-nine human proportions increase or decrease during growth for 32.2 per cent of their values in the fetus, whereas the same proportions of the gibbon change for only 24.8 per cent of their initial values.

The average relative ontogenetic changes in the eleven proportions, which are available in all primate fetuses and adults, show the following values:

Man	Gorilla	Chimpanzee	Gibbon	Orang-utan
23.4	9.8	7.9	7.7	6.7

According to these last figures, which are based exclusively upon limb proportions, man changes in the course of growth much more extensively than any of the apes. It is also noteworthy that of all the apes gorilla comes nearest to man in

<sup>27</sup> The average relative ontogenetic change is expressed by the following formula:

$$\left[ \sum \frac{fx - ax \text{ (or: } ax - fx)}{fx} \times 100 \right] : n$$

*fx* = value of a proportion in the fetus; *ax* = value of the same proportion in the adult of the same primate species; *n* = number of proportions considered.

this respect. In all of the apes the limb proportions change ontogenetically on an average for less than one-tenth of their values in fetal life, but in man this change amounts to nearly one-fourth of the fetal values. To find this marked contrast between the apes on the one hand and man on the other is rather unexpected. This result encourages further investigations of this important problem. It is not at all unlikely that it will be possible to demonstrate a direct connection between the amount of ontogenetic change and the duration of growth. At present it must suffice to point out that among higher primates it is one and the same form—man—which has its proportions changed most extensively during development and which possesses the longest period of growth, by which, one may add, it has become possible to accomplish these unique changes.

Finally, it should be mentioned that the above data do not agree with the recent stimulating theory of Bolk (1926 a & b) which supposes that man is distinguished from the apes by retaining fetal conditions more closely than do the latter. In regard to most body proportions just the opposite seems to be the case, as shown by the following two examples in addition to the averages discussed above. The important relation in length between upper and lower limb (i 26, Table 8) changes in man from 114 in the fetus to 82 in the adult, or for 28.1 per cent of the fetal value, but in gorilla it changes only from 151 in the fetus to 141 in the adult, or for only 6.6 per cent of the fetal value which is less than one fourth the relative amount in man. The proportion between the size of head and trunk (i 33) decreases in man from 78 in the fetus to 31 in the adult, or for 60.3 per cent of the former value. In the gibbon the same proportion drops only from 61 to 48, *i.e.*, for only 21.3 per cent of the index in the fetus. In both these instances the apes retain the fetal condition much more closely than does man.

#### PART IV.

##### Chapter 12. SUMMARY AND CONCLUSIONS.

The results obtained from this study refer to a wide variety of topics with frequently little, if any, connection between the points discussed. This paper, therefore, can not claim to present a coherent picture of the conditions of growth in gorilla and other higher primates. It constitutes merely a first attempt to bring together the previously scattered observations of other authors and to fill, as far as possible, some of the gaps in this collected information. This effort shows first of all how little exact knowledge of the ontogeny of apes is really as yet available, and how much more material and study will be necessary before all the outlines at least of this important chapter of science can be definitely established.



The following enumeration of the most noteworthy data, derived from the present investigations, deals in part with final and amply supported facts, but in part also with only tentative findings, requiring corroboration from observations on additional specimens.

*General conditions of growth.*

The African apes grow more slowly than man before birth but much more rapidly during postnatal life. The total period of growth is very much shorter in apes than in man and the relative amount of growth-change in body-proportions is markedly less in the former than in the latter.

*Body surface.*

The first pigment of the skin of higher primates appears often in localized zones. The color of the skin develops earlier in the orang and the chimpanzee than in the gorilla. The latter occupies an intermediate position in this respect between the former and the negro. In all the apes and in negroes the final and darkest color of the skin is not attained until shortly after birth.

As in man, the first hair of the gorilla appears on the eyebrows, lips and chin; the eyelashes and the hairs on the scalp develop slightly later. Man, the gorilla, and the chimpanzee have in common the fact that during late fetal life and earliest infancy the hair on the scalp is very much longer than on the rest of the body. In new-born lower primates there exists no such difference between the length of the hair of the head and that of the hair on the body.

The ischial callosities of catarrhine monkeys develop relatively early in fetal life and before any hair has appeared over the ischial tuberosities. In the gibbons these callosities appear at a much later stage of growth, replacing a coat of very short hair. The latter disappears late in fetal life from two symmetrically placed zones. Not until shortly before birth does the skin of these zones begin to become callous. Such hair-free zones have been observed in an older chimpanzee fetus. In rare cases anthropoid apes may still possess ischial callosities. These are less developed and less frequent in the gorilla than in the chimpanzee and orang, indeed, in the gorilla they may really no longer deserve the term "callosity". Another kind of callosity, one which occurs in connection with their special mode of walking, is found in the gorilla and the chimpanzee on the middle segments of the fingers. These callous places and the associated lack of hair over the middle phalanges have been found in fetuses of both these apes and are, therefore, hereditary characters.

The coccygeal tubercle, the last ontogenetic remnant of an outer tail, disap-

pears at a much earlier stage of development in man and gibbon than in the gorilla, orang, and chimpanzee. Among the last three apes this structure persists for the longest period in the chimpanzee and for the shortest in the gorilla.

In the females of all the higher primates the labia majora are well developed in fetal life, but, whereas they persist in man and the gibbon throughout life, they undergo during postnatal growth a process of nearly, or even entirely, complete reduction in the three large apes.

Accessory folds on the eyelids of anthropoids and the marked general wrinkling of the skin in the region of the eyes develop in apes during fetal growth. In man, on the other hand, such wrinkling does not appear until very late in life, if it occur at all.

The lips of gorilla fetuses are still as broad as in negro fetuses, but in the former this condition does not persist as in the latter.

#### *Body proportions.*

Of all the body proportions those of the limbs show the greatest differences among the various higher primates, whereas those of the trunk are most similar in apes and man. The relative circumference and widths of the trunk of higher primates decrease in general with advancing development. In the gorilla there seems to exist a tendency to increase the relative girth of the chest late in growth. The trunk of lower primates is long and slender, but that of apes and man is proportionately broad and stout and even more so in the gorilla than in man.

The length of the upper limb in relation to the height of the trunk increases in most primates during the first part of growth but decreases slightly during the second part. The lower limb-length of the gorilla grows somewhat faster than the height of the trunk and also slightly faster than the length of the upper limb. *Gorilla beringei* has on an average somewhat shorter upper and somewhat longer lower limbs than has *Gorilla gorilla*. In gorilla the forearm is relatively shorter than in any other ape. It is especially short in *Gorilla graueri*, which equals man in regard to the humerus-radius proportion. The hand of the adult gorilla is relatively shorter and broader than that of other apes and equals in these respects the human hand. In regard to the relative size of the thumb the adult gorilla, particularly *Gorilla beringei*, resembles human conditions more closely than do other apes. The foot of the adult gorilla is extremely broad; the heel is broad and prominent; the great toe reaches relatively far forward; and the lateral toes are relatively short. In all these features gorilla approaches man more closely than do other apes. In *Gorilla beringei* the great toe and the sole extend proportionately further forward than in *Gorilla gorilla* and the cleft between toes I and II as well



as the lateral digits are shorter in the former than in the latter. In the gorilla fetus the hand as well as the foot is of a much more arboreal character than it is at the completion of growth. Both hand and foot are relatively longer and more slender, the thumb as well as the great toe is proportionately shorter, and digits II to V are proportionately longer in the fetus than in the adult.

The size of the head decreases with advancing growth in proportion to the size of the trunk in the gorilla as well as in all other primates. Fetuses of apes and man have extremely broad heads, *i.e.*, very high cephalic indices. The nose is as prominent in gorilla fetuses as in negro fetuses and it projects more in all later stages of growth in the gorilla than in the other apes. The ear of gorilla increases with advancing development in relation to the size of the head.

*Comparisons based upon deviation indices.*

In regard to body proportions man rarely falls within the range of the different values for the same character among the apes, but most frequently represents one extreme of the total range of all higher primates. Within the latter range, however, there exist just as marked differences between one ape and another ape as between some one ape and man. The resemblance between the various higher primates is much greater in fetal than in adult life. Fetuses do not as yet show the wide divergences of adults, but are much more uniform in regard to body proportions than the latter. Of all the apes gorilla resembles man most closely, both in fetal and in adult life. The chimpanzee ranks second in this respect, whereas the two strictly arboreal apes, the orang and gibbon, are much further removed from man than are the African apes.

The statement in the last paragraph, that there exists a greater similarity between man and gorilla than between man and any of the other apes, is supported not only by the average and maximum deviation indices, but also by many other findings of the present study. Some of these corroborative findings, which are not considered in the deviation indices, may be briefly reviewed again: Ischial callosities are no longer present in man; they may be merely indicated in the gorilla in very rare instances; but in the chimpanzee and orang they are still quite well developed in occasional specimens. The color of the skin of the gorilla develops somewhat earlier than that of the colored races of man, but in the chimpanzee the skin begins to darken at a still earlier stage than in the gorilla. The relative amount of ontogenetic change is greatest in man, but in gorilla it is greater than in the other apes. Horizontal sections through the nasal region of the skull are straight, indicating a flat nose in the gibbon, orang, and chimpanzee; but they are curved forward, according to the prominence of the nose, in the gorilla and

man. The size of the gorillan ear is in general quite similar to that of the human ear; whereas the ear of the orang is very much smaller, and the ear of the chimpanzee very much larger, than the ears of the former two primates. The points of similarity in the hand and foot of man and the gorilla, particularly of *Gorilla beringei*, are too numerous and detailed to repeat here. There can be no doubt that in regard to hand and foot no other ape can rival the gorilla in its claim to being least different from man. Last, but not least, must be mentioned that in general mode of life man, the exclusively terrestrial primate, has become far removed from the apes. Again, however, it is the gorilla which differs in this respect from man to a lesser degree than do the other forms, since the adult gorilla is largely terrestrial, the chimpanzee largely arboreal, and the orang as well as the gibbon extremely arboreal.

That the last mentioned distinctions were much less pronounced in the past, and did not as yet extend to the extreme modes of life, may be concluded from certain ontogenetic conditions, particularly from those appertaining to the limbs. Observations on human fetuses, published by the author in previous papers (1924 a, 1925, 1926 b), justify in his opinion the conclusion that man's evolutionary course must have passed from arboreal through semi-terrestrial to extremely terrestrial phases. On the other hand, the as yet unfinished studies of the author on the growth of the orang-utan and the gibbon permit the preliminary deduction that the *extreme* adaptations to tree-life, which distinguish these apes, had not yet been developed in earlier phases of their phylogeny. Finally, the present investigation has produced evidence in support of the assumption that the gorilla has changed comparatively recently from an arboreal to a largely terrestrial mode of life. It has been shown that the hand and the foot of gorilla possess in late fetal stages most of the features typical of arboreal, though not extremely arboreal, primates. Even in gorillan infants these structures are not yet nearly as much modified for terrestrial use as in adults. Furthermore, in the adult of this ape the arms are proportionately shorter and the legs relatively longer than in the young animal. This all rather strongly suggests that, while attaining its unique colossal size, which rendered tree-life impracticable, the gorilla swerved in its evolutionary trend toward that which was most likely followed by the human precursors. This change seems to have been somewhat more pronounced, or to have been more accelerated, in *Gorilla beringei* than in the West African gorillas. In this connection there should be quoted a conclusion reached by Gregory (1916), with which the above statement agrees very well, but which points out in addition the important inherent limitations to the evolutionary course of the gorilla: "In



adopting a partly terrestrial habit the gorilla has entered upon a line of adaptation which in the forerunners of man resulted in a fully bipedal, cursorial type, capable of invading the plains. But, as the gorilla is largely frugivorous and limited to the forests and their neighborhood, the only course left for it (apart from its inevitable extinction by man) would have been to go on increasing still further in size, until it might have surpassed even the Kadiak bear in bulk. Such a beast might have ambled along on all fours, partly supporting itself upon its knuckles as the gorilla now does."

The particular conclusion that the difference between man and gorilla is less than that between man and other apes does not necessarily imply that man

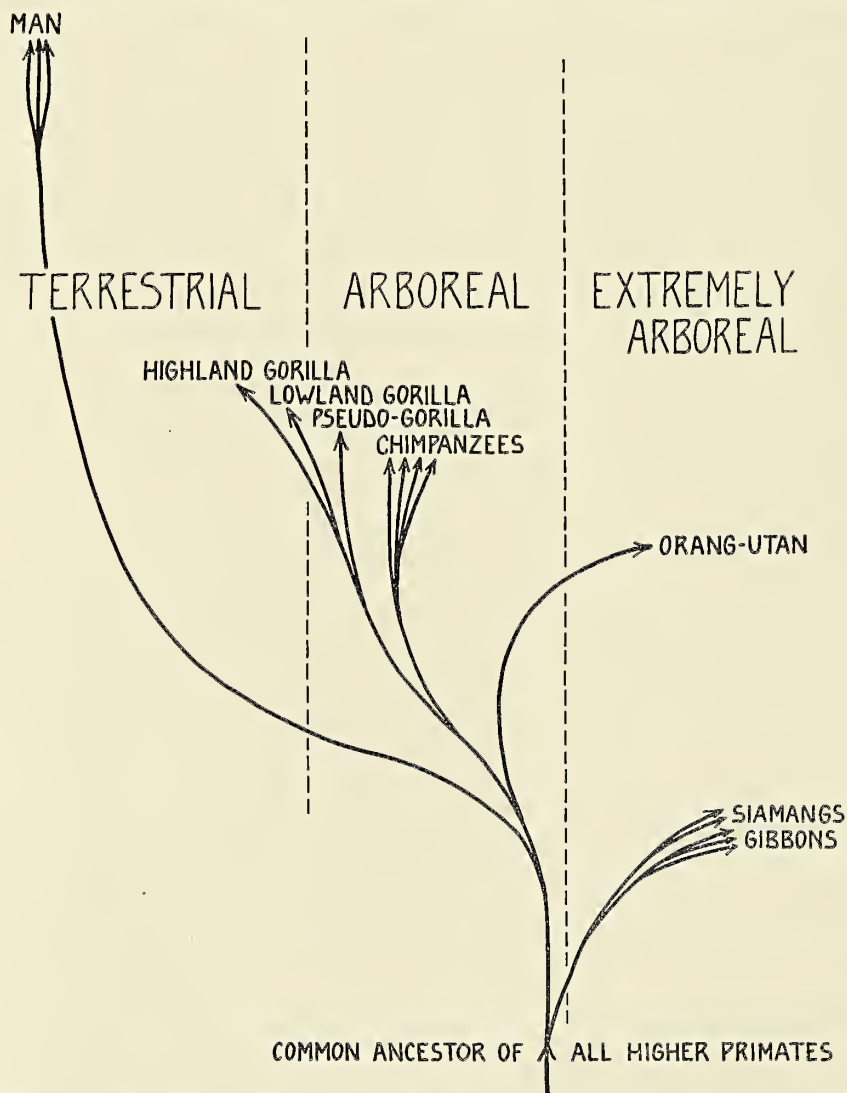


Fig. 6. Hypothetical pedigree of the recent higher primates, as supported by the results of this paper. The branching lines indicate in their directions and relative lengths the probable degrees of divergence in the various evolutionary trends and the proportionate amounts of general departure from the common ancestral form.

descended from gorilla-like forms, nor that a common ancestor of the two resembled the gorilla, though such structures as the foot and such proportions as that between the lengths of upper and lower limb were most likely gorilla-like in some stage of man's evolution. It must mean, however, that the evolutionary courses of man and the gorilla diverged to a lesser degree than did the ascending paths of man and the other apes. All the higher primates must have undergone far-reaching changes since they spread from a common source. For reasons to discuss which here would lead too far, the author is inclined to the view that in many respects (excluding all the *extremely* arboreal specializations) the gibbons departed least from the ancestor of all the higher primates and even stand closest of all recent primates to the hypothetical form which links man with the three large apes. These ideas are represented in diagrammatic form in text-figure 6. It must be stated emphatically that this particular pedigree is based principally upon body proportions and the other topics discussed in this paper. As has been mentioned in the introduction, the final family tree will have to consider the evidence from all the fields of biology. It will, therefore, represent to a certain degree a critical compromise between all the pedigrees suggested independently by different specialists. Naturally, the last word will have to be granted to paleontology, even though its testimony be restricted to the skeleton and the teeth.

The particular pedigree, proposed here, agrees in principle with that published by Keith (1925); but differs slightly from those of Gregory (1916), Sonntag (1924), and others, inasmuch as according to the latter pedigrees, the orang branches off before man does, and according to the diagram here given this relation is reversed. The author's diagram is based upon the study of recent primates alone, from which it seems at present impossible to abandon the view that in general the three large apes are linked somewhat more closely together than man and the African apes.

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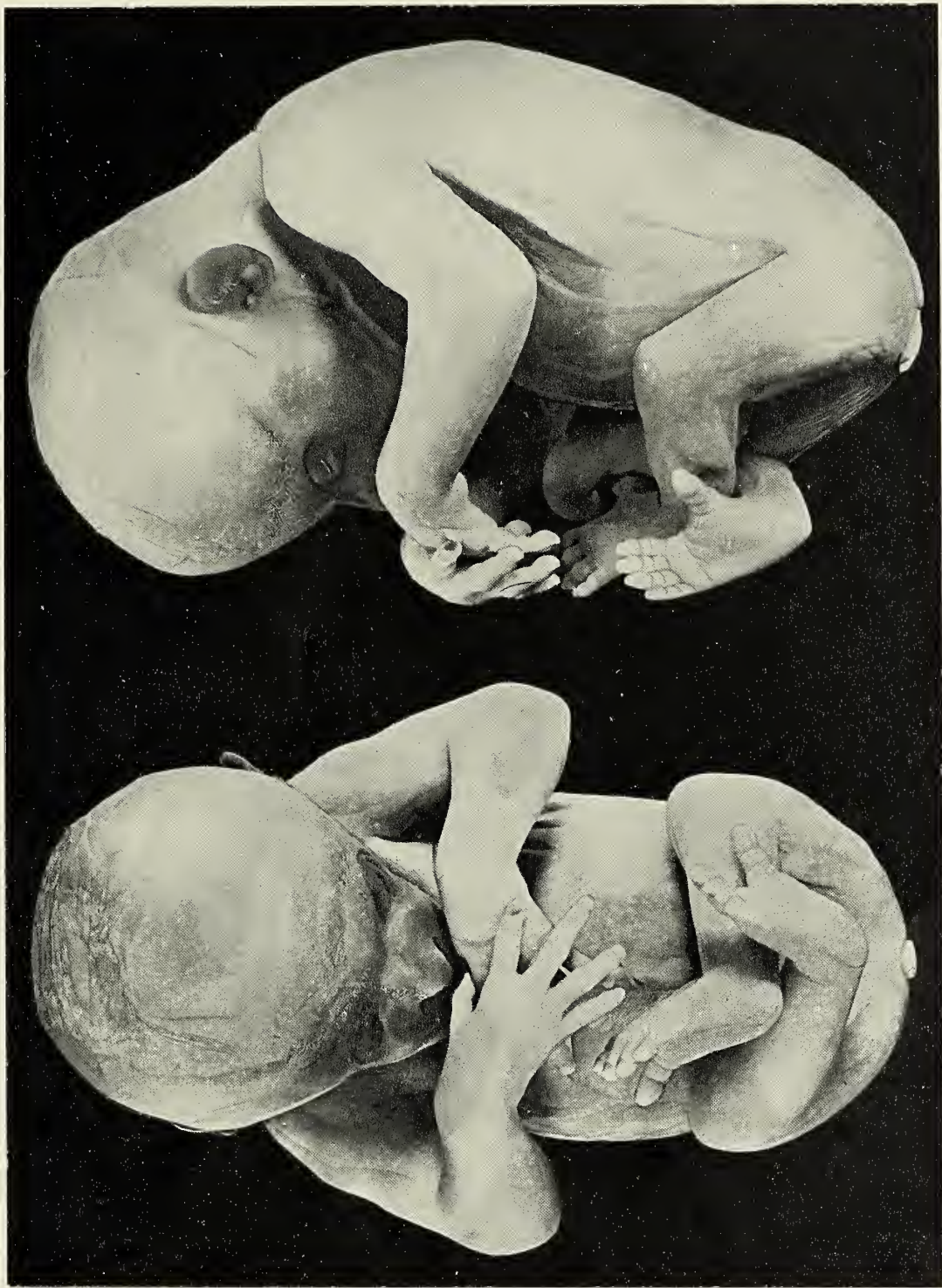
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## EXPLANATION OF PLATE I

Front and side view of Gorilla Fetus II (approximately natural size.)  
Car. Mus. Acc. No. 7698.



Gorilla Fetus II. Natural Size.









## EXPLANATION OF PLATE II.

- FIG. 1. Front view of Gorilla Fetus V (after Anthony, 1918).  
FIG. 2. Side view of Gorilla Fetus III (after Deniker, 1885).  
FIG. 3. Gorilla VI at the approximate age of one month, with its negro nurse, (after Reichenow, 1921).



1



2



3

(For explanation of plate see opposite page.)





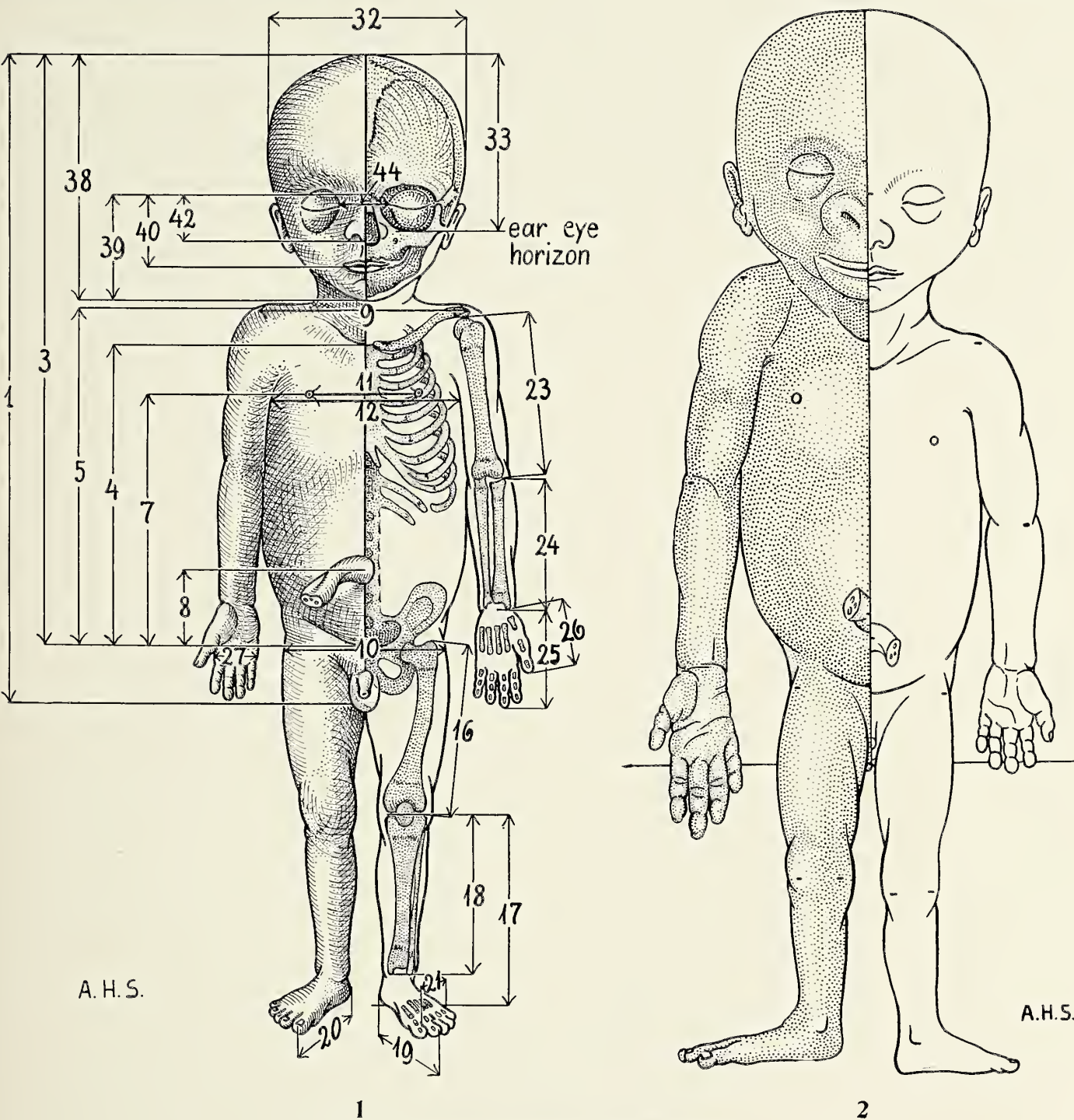




## EXPLANATION OF PLATE III.

FIG. 1. Diagram of measurements. Human fetus with parts of skeleton shown on one-half of the body. The numbers refer to the serial number of the particular measurements.

FIG. 2. Diagrammatic representation of exact body proportions of Gorilla Fetus II (gray half) and of average proportions of human fetuses (series 1) of corresponding development (white half). The horizontal line marks the lower end of the sitting height. The figure is based upon the measurements in Table 1.



(For explanation of plate see opposite page.)









## EXPLANATION OF PLATE IV.

FIG. 1. Front views of heads of juvenile gorilla (after Klaatsch, 1911) and of juvenile chimpanzee\* (Collection of Department of Anatomy, Johns Hopkins University).

FIG. 2. Perineal region of the female Gorilla Fetus II and of a female human fetus of corresponding development. 1 = clitoris; 2 = labia majora; 3 = anus; 4 = coccygeal tubercle.

FIG. 3. Developmental changes in the external female genitalia of gibbon. *A* = fetus of *Hylobates mülleri*, sitting height 100 mm.; *B*. = fetus of same species, sitting height 161 mm.; *C*. = nearly fullgrown *Hylobates agilis*. 1 = clitoris; 2 = labia minora; 3 = labia majora; 4 = anus; 5 = ischial callosity.

\* This chimpanzee, after its death, was generously sent to the author by its former owner, Mr. J. L. Buck. It is a rather unique specimen, the species of which could not be determined. It has a very broad conspicuous nose of a light blueish-gray color, very long and dense black hair, and unusually short limbs. In a recent article (1927) Mr. Buck mentions this specimen under the name "Bosambo" and expresses the opinion that it is a gorilla-chimpanzee hybrid. However, a careful study of the preserved animal leaves no doubt that it is a true chimpanzee, but perhaps, of a new species.



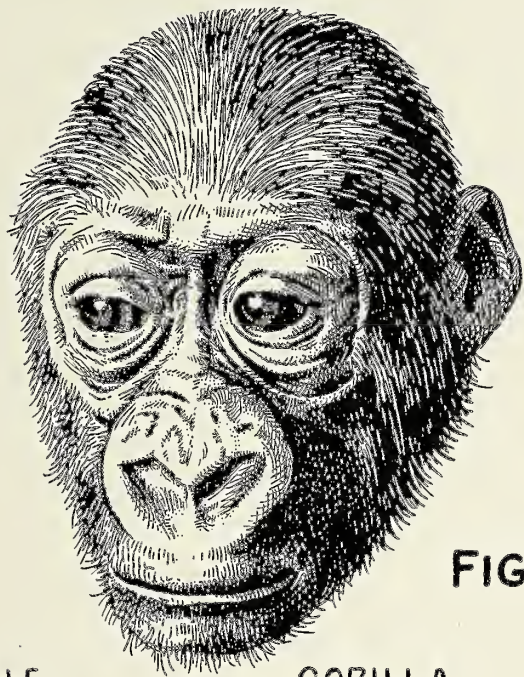
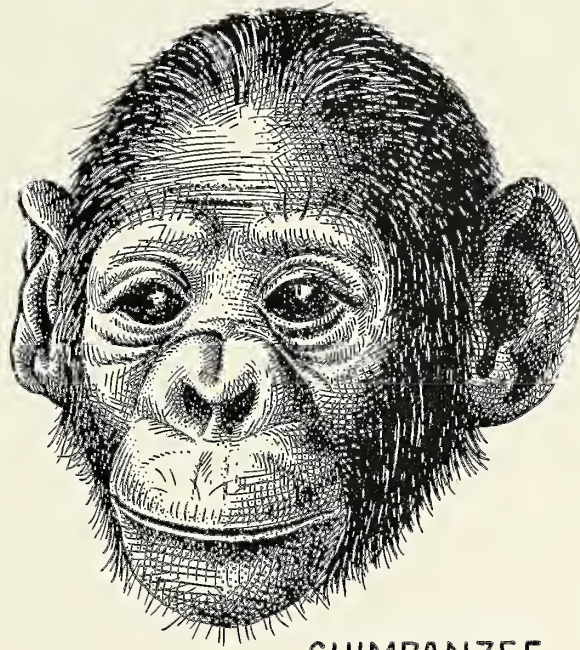


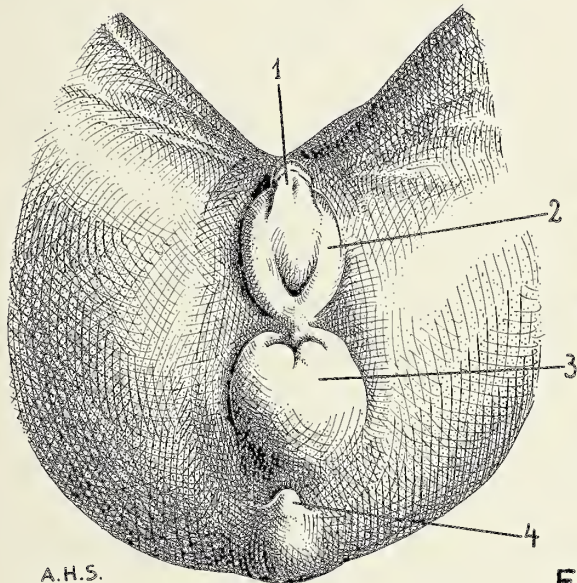
FIG. 1

A.H.S.

GORILLA



CHIMPANZEE



A.H.S.

GORILLA, ♀

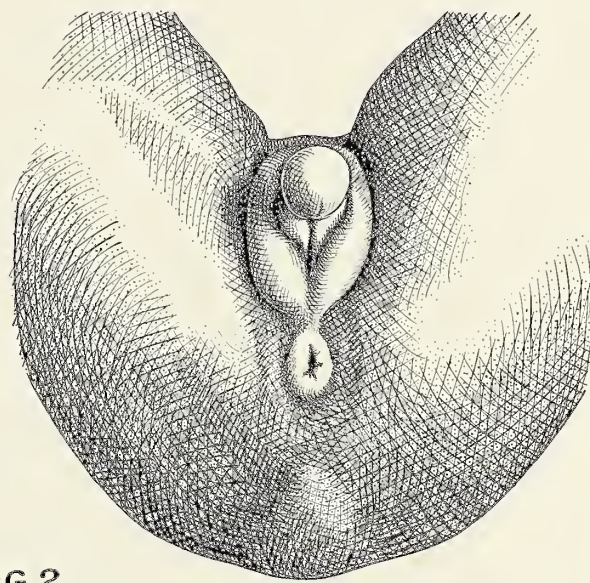
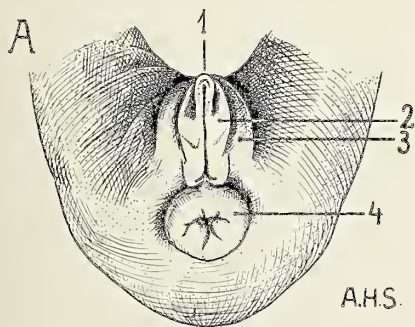


FIG. 2

MAN, ♀



A.H.S.

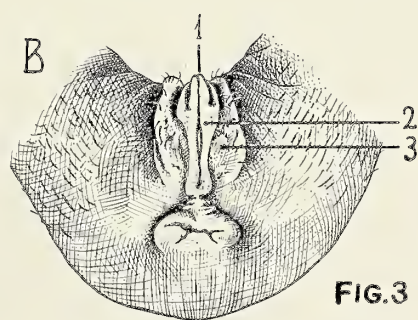
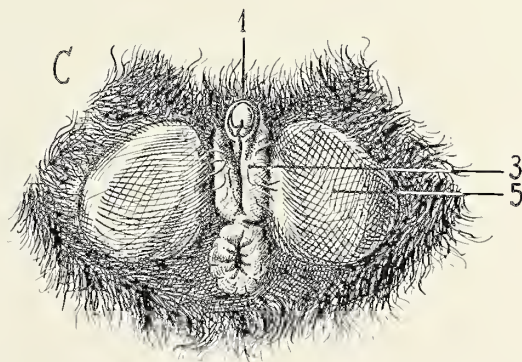


FIG. 3



(For explanation of plate see opposite page.)

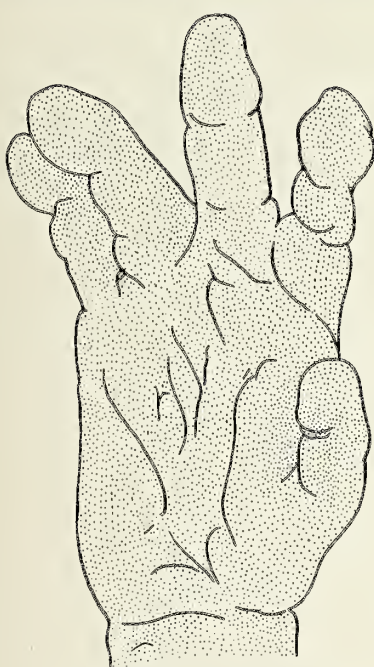




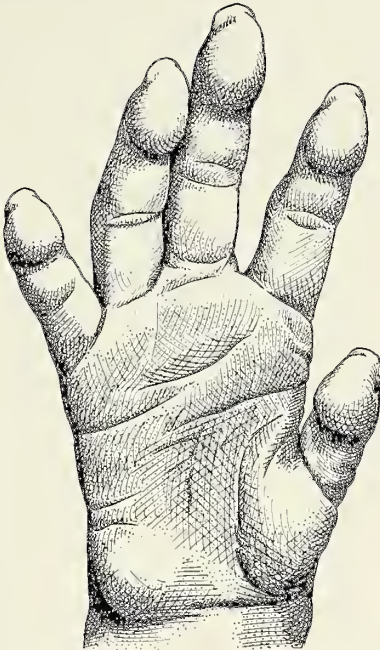


## EXPLANATION OF PLATE V.

Hands of gorilla, all reduced to the same total length. Upper row: fetuses I, II, and III; lower row: adult *G. Gorilla* after Hartmann (1880) and adult *G. beringei* (♀), drawn from a copy of a plaster cast, of which the original was made and published by Akeley (1923).



I. (DUCKWORTH)



II. (SCHULTZ)

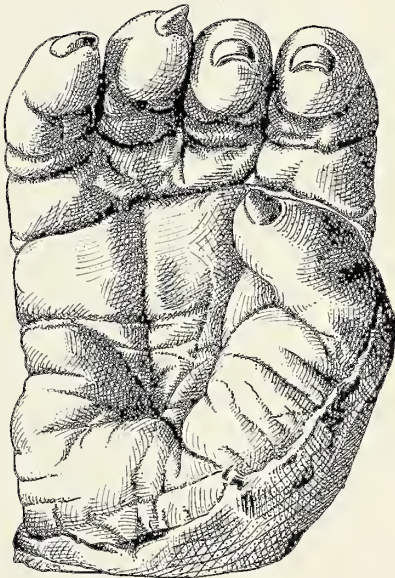


III. (DENIKER)



A.H.S.

ADULT (HARTMANN)



ADULT (AKELEY)

(For explanation of plate see opposite page.)







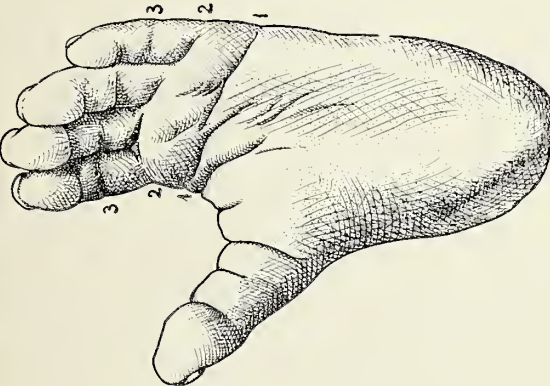
## EXPLANATION OF PLATE VI.

Feet of gorilla, all reduced to the same total length. Upper row: fetuses I, II, and III, five year old male (drawn from a cast of "John Daniel I" by Prof. McGregor), and adult *Gorilla gorilla* (after Hartmann, 1880); it is possible that this gorilla is not entirely adult. Lower row, *left*: feet of negro fetuses of the fifth month, showing the maximum and the minimum relative toe-length of a considerable series of specimens: *right*: adult female *Gorilla beringei* (drawn from a copy of a plaster cast of which the original was made and published by Akeley, 1923) and adult *Gorilla gorilla* (after Brehm, 1876). Distance  $A_1-B$  or  $A-B$ =length of cleft between toes I and II; distance  $A-C$ =total foot-length; 1, 2, and 3=flexure folds, for explanation of which see text.

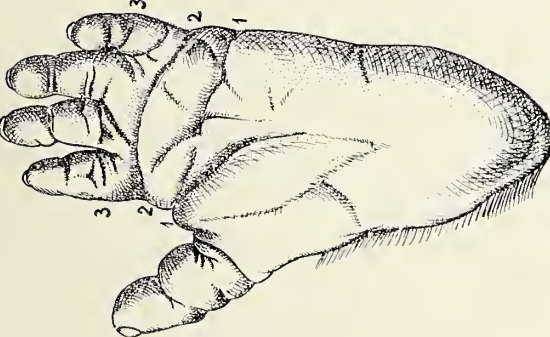




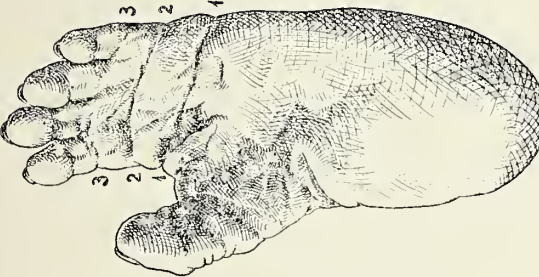
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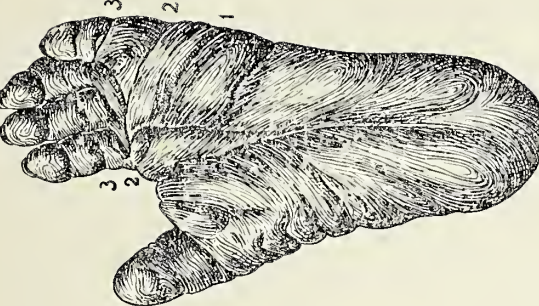
II. (SCHULTZ)



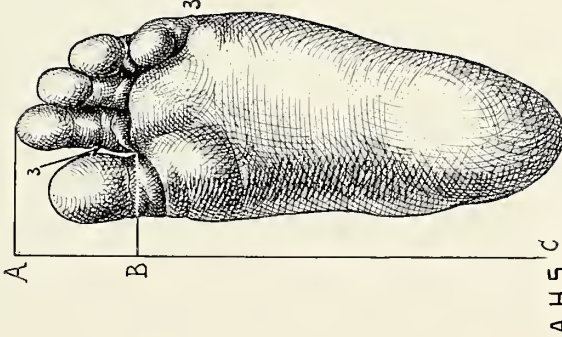
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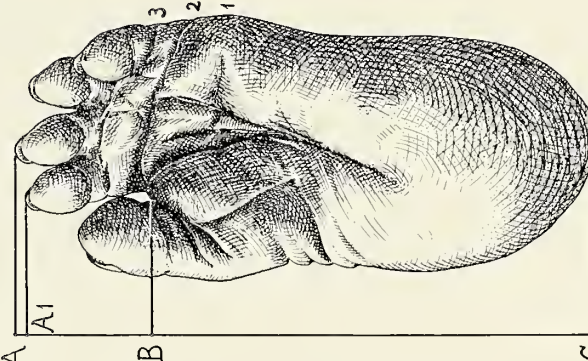
5 YEARS OLD



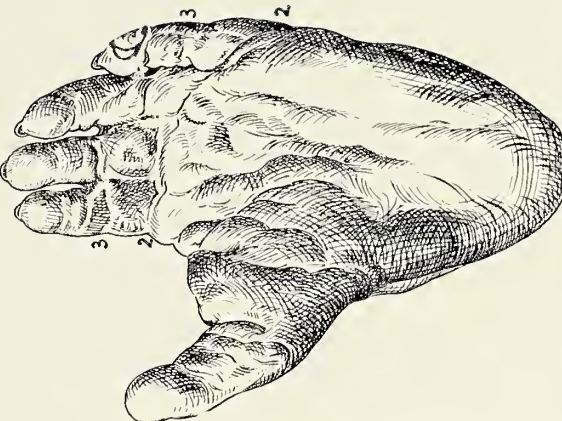
ADULT (HARTMANN)



HUMAN FETUSES, 5TH MONTH



ADULT (AKELEY)



ADULT (BREHM)

(For explanation of plate see opposite page.)



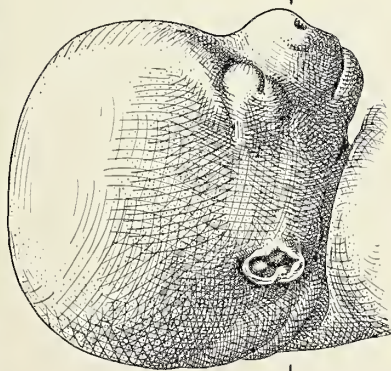




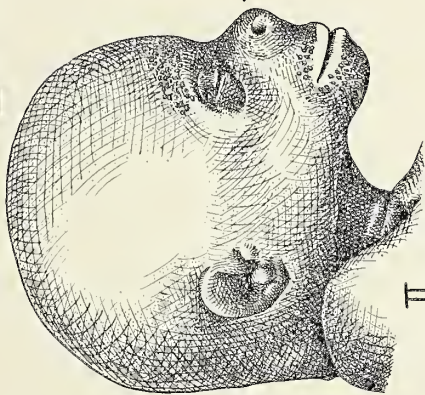
## EXPLANATION OF PLATE VII.

FIG. 1. Side views of heads, all reduced to approximately the same size and oriented according to their ear-eye horizons (the head of Deniker's fetus is probably slightly tilted to the specimen's left side). Upper row: gorilla fetuses I to IV. Lower row: negro fetuses (I corresponding in development to gorilla fetus I; II corresponding to gorilla fetus II) and infantile gorilla (after photograph).

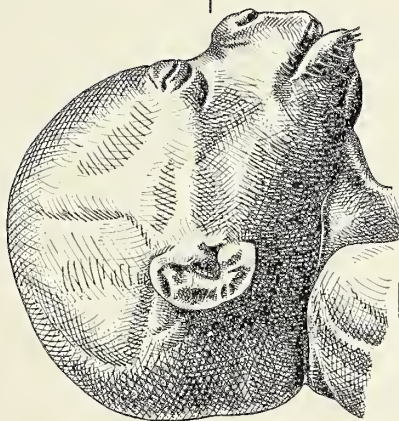
GORILLA FETUSES



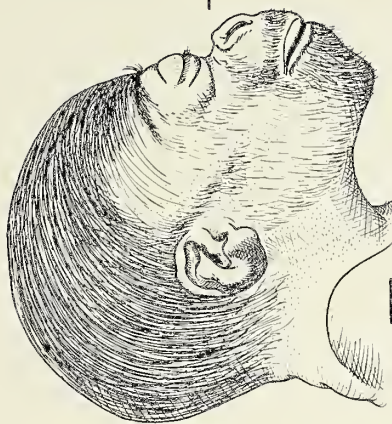
I.  
(DUCKWORTH)



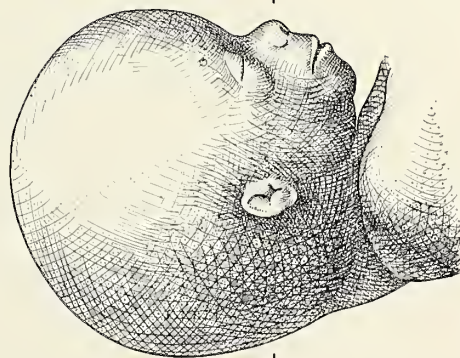
II.  
(SCHULTZ)



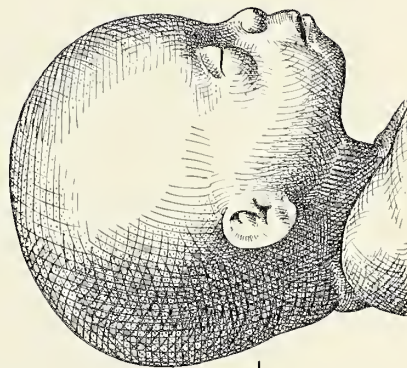
III.  
(DENIKER)



IV.  
(BOLK)

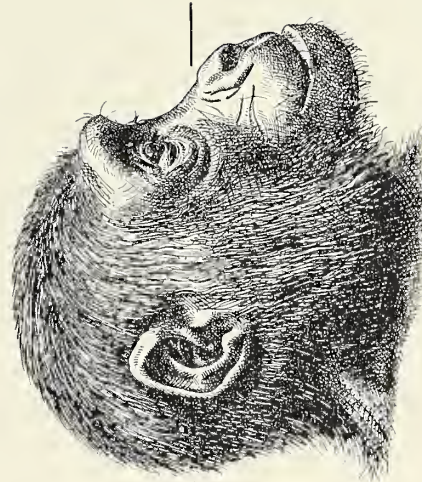


A.H.S.  
I.



II.

NEGRO FETUSES



GORILLA INFANT

— EAR-EYE HORIZON —

(For explanation of plate see opposite page.)





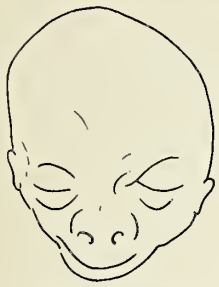


## EXPLANATION OF PLATE VIII.

Fig. 1. Front views of heads of anthropoid fetuses and infants, all reduced to approximately the same size. Upper row: gorilla fetuses I to IV and infant VI. Lower row: chimpanzee fetus (No. 2, chapter 2), orang fetuses (from the collection of the U.S. National Museum), newborn chimpanzee (after Blair, 1920). The fetuses in the lower row correspond in development approximately to the fetuses perpendicularly above them in the upper row. Judging by the high position of the ears, the heads of fetuses I and IV are tilted forward.

FIG. 2. Front views of skulls of juvenile and adult apes and man (oriented in Frankfort horizon and drawn with dioptrograph). The juvenile and the adult chimpanzee are males; the adult gorilla is a female; the adult negro skull comes from eastern Senegal and is that of a female; the adult white skull is that of a male Swiss Alpine. The two gorillas belong to the collection of the Anthropological Laboratory of the Johns Hopkins University; all the other skulls are in the author's private collection. The thick curves, marked *a* and *b*, represent horizontal sections through the nasal region at the levels indicated by straight lines (*a* and *b*) on the front views of the skulls. Level *a* is determined by the fronto-maxillary suture; level *b* by the lower end of the nasal bones. The section curves were drawn with Martin's diagraph (Martin, 1914) and enlarged to twice the scale of the front views of the skulls. The orbital portions of the curves (*a*) are drawn in thinner lines than the interorbital part.

GORILLA



I. (DUCKWORTH)



II. (SCHULTZ)



III. (DENIKER)



IV. (BOLK)



2 MONTHS (REICHENOW)



A.H.S.

CHIMPANZEE (FRIEDENTHAL)

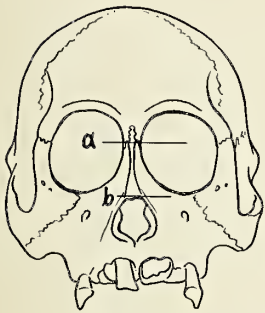


ORANG-UTAN (SCHULTZ)



CHIMPANZEE (BLAIR)

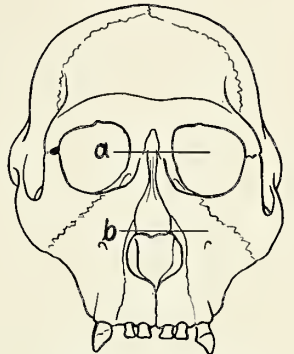
1



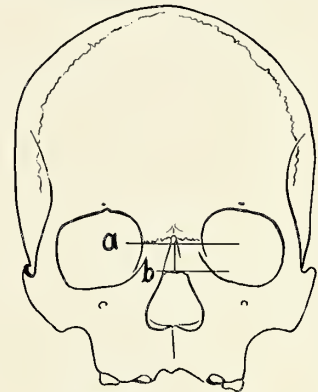
ORANG, JUVEN.  
a b



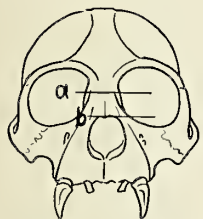
CHIMPANZEE, JUVEN.  
a b



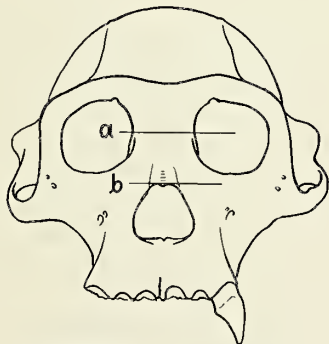
GORILLA, JUVEN.  
a b



NEGRO, ADULT  
a b



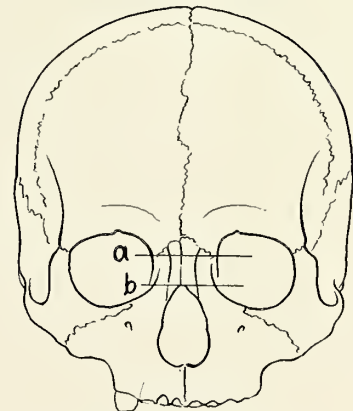
SIAMANG, ADULT  
A.H.S.  
a b



CHIMPANZEE, ADULT  
a b



GORILLA, ADULT  
a b



WHITE, ADULT  
a b

2

(For explanation of plate see opposite page.)





MEMOIRS  
OF THE  
CARNEGIE MUSEUM

VOL. XI

No. 2.

W. J. HOLLAND, EDITOR

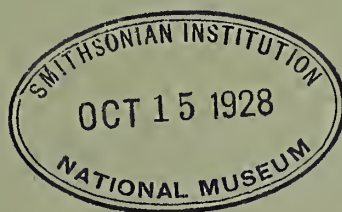
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THE BROWN'S PARK FORMATION

By O. A. PETERSON

(Plates IX-XV)

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April 8, 1928





# MEMOIRS

OF THE

## CARNEGIE MUSEUM

VOL. XI.

No. 2.

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### THE BROWN'S PARK FORMATION<sup>1</sup>

BY O. A. PETERSON.

(PLATES IX-XV)

#### INTRODUCTORY

In the northwestern corner of the state of Colorado, covered by Moffat County, there is located a Tertiary formation of considerable geographical extent, the geological age of which for many years has been the subject of discussion among geologists. Hayden in his "Preliminary Report of the United States Geological Survey of Wyoming and Portions of Contiguous Territories," 1871, p. 64, states that these sediments are of Pliocene age, while King (U. S. Geol. Sur. 40th Paral., 1877, p. 222) regarded the beds as most nearly allied to the Green River group, to which he referred them.<sup>2</sup> Sinclair in his paper on the "Volcanic Ash in the Bridger Beds of Wyoming," regards the Bishop (Wyoming) Conglomerate as probably Pleistocene, (Bull. Amer. Mus. Nat. Hist., Vol. XXII, 1906, p. 278).

Until within the past year the age of the Brown's Park Formation has remained uncertain. In a paper published as late as 1924<sup>3</sup> Sears quotes Douglass as believing the formation to be probably of Miocene age, and also quotes Peterson as saying that he believed the deposits to be probably of lower Miocene age, although

<sup>1</sup>Major J. W. Powell in his report on the Geology of the Uinta Mountains used the name "Brown's Park Formation" (U. S. Geol. and Geogr. Survey of the Terr. 1876, p. 4).

<sup>2</sup>In other places in King's report he suggests the possibility that these beds may be one of the later Tertiary formations. King was perhaps partly influenced in making these suggestions by Hayden's original statements in his report of 1871.

<sup>3</sup>Sears, Julian D., Bull. Geol. Soc. of America, Vol. XXXV, 1924, p. 287.

they may belong to the uppermost Oligocene. In 1924<sup>4</sup> Peterson described some fossil mammalian remains from the Brown's Park beds as of lower Miocene age, but the closing sentence in the introduction to his paper informs the reader that the determination of the age of the Brown's Park sediments should be regarded as provisional, "subject to verification upon the discovery of more complete paleontological evidence." From an abstract of Peterson's paper, forwarded to T. W. Stanton as a personal communication, Stanton in a foot-note to a paper by E. T. Hancock<sup>5</sup> states that Peterson regards the Brown's Park formation as being probably lower Miocene.

White in the Tenth Annual Report of the United States Geological and Geographical Survey, 1878, p. 38, in speaking of the Brown's Park sediments says: "The relation which this group has to similar groups in different parts of that great western region remains for future investigation to determine, its relation to those [beds] immediately associated with it is a matter of great interest, which will be much enhanced by any paleontological testimony that its strata may yet furnish." In consulting the numerous reports upon the Brown's Park formation, from that of Hayden in 1871 to and including that of Hancock in 1925 (*l. c.* pp. 24-25), it is quite clear that all made a diligent search for fossil remains in the Brown's Park beds with little or no success. During the summer of 1923 Messrs. Douglass and Kay in the employment of the Carnegie Museum discovered near Sunbeam, Colorado, in the Brown's Park sediments the first mammalian remains sufficiently perfect to permit of description.<sup>6</sup> In 1925-1926 the field party in charge of Mr. J. LeRoy Kay was so fortunate as to secure additional mammalian remains in the Brown's Park sandstones. The purpose of this paper is to give a short review of the geology of the Brown's Park and Bishop Conglomerate beds and to describe this additional material. This is undertaken with a view to assisting geologists in placing the two formations mentioned in their relative sequence in the Tertiary strata of our western states.<sup>7</sup> Judging from the fauna described in this paper the Brown's Park formation seems to be near the geological age of such Miocene and Pliocene formations as the Pawnee Creek of Colorado, the Madison Valley, probably the Flint Creek and Deep River of Montana; the Santa Fe of New Mexico; the Mascall of Oregon, and the Virgin Valley of Nevada.

<sup>4</sup>Peterson, O. A., *Ann. Car. Mus.*, Vol. XV, 1924, pp. 299-305.

<sup>5</sup>Hancock, E. T., *Bull. 757 U. S. Geol. Surv.* 1925, p. 25.

<sup>6</sup>*Ann. Car. Mus.* Vol. XV, 1924 pp. 299-304. A review of this work will appear in the present publication.

<sup>7</sup>A preliminary note by O. A. Peterson was published in *Science* (N. S.) 63, 1926, p. 231, calling attention to the discovery of a long-jawed proboscidean in the Brown's Park formation, and also stating the view that it represents the Upper Miocene and Lower Pliocene.



The very important role, which the Brown's Park and Bishop Conglomerate formations played in shaping the courses of the Green and Yampa rivers through canyons of the Uinta and Yampa uplifts, is fully recognized as an extremely tempting question for discussion. However, before entering upon this theme a much longer time than I have been able to devote to work in the field is obviously necessary in order to finally pass upon the many previous observations of others. Nevertheless I may in passing say that according to the present state of my knowledge of the geology of the Uinta and Brown's Park basins I am strongly inclined to the view of Emmons,<sup>8</sup> Hancock,<sup>8</sup> Sears,<sup>8</sup> and others that the courses of the Green, the Vermillion, the Snake, and Bear rivers were established on the Bishop Conglomerate and Brown's Park formation as against the hypothesis of J. W. Powell<sup>9</sup> and others who maintained that these rivers already existed in their present channels before the deposition of the formations which we are studying.

The writer takes pleasure in expressing his gratitude to Mr. William Weller on whose ranch the greater part of the material was found, and who not only extended hospitality, but gave cordial assistance to Mr. J. LeRoy Kay who collected the fossil remains, and materially helped in obtaining the cross-sections, contact sections, and other data. Special thanks are due to Mr. Childs Frick for his financial assistance which enabled me to make my trip to the Brown's Park region during the summer of 1926. I acknowledge the kindness of Professor Henry Fairfield Osborn, who allowed me to use an unpublished illustration for comparison in connection with the description of a Pleistocene elephant from Lay Creek, Moffat County, Colorado; and of Dr. J. D. Figgins, Director of the Colorado Museum of Natural History, Denver, Colorado, for permission to identify and describe a proboscidean molar tooth from western Colorado, the property of the Denver Museum, and of Dr. Charles C. Mook for assistance in the identification of a Pleistocene proboscidean. I am indebted to Director A. Avinoff for helpful suggestions in my work, and for making the restoration shown on Plate XV in this paper, the illustrations of which are chiefly from drawings made by Mr. S. Prentice. I desire to recognize the skill of Mr. S. Agostini who extracted from the matrix and prepared the material from Brown's Park for study and exhibition. Finally I wish to express my indebtedness to Dr. W. J. Holland, who has revised and edited this paper, as in times past he has revised and edited many others for the writer.

<sup>8</sup>U. S. Geol. Expl. 40th Par., vol. 2, 1877 pp. 194, 187; U. S. Geol. Survey Prof. Paper 90, 1915, pp. 183, 189; Bull. Geol. Soc. of America, Vol. 35, 1924 pp. 279-304.

<sup>9</sup>Exploration of the Colorado River of the West and its tributaries. 1875. pp. 152-153.



## GEOGRAPHY AND ROUTES OF TRAVEL.

The Brown's Park Formation rests in a long, narrow, irregularly shaped basin, and is bounded by the Uinta Mountains to the southwest, by the Cold Spring Mountains to the northwest, by a low ridge and the Cedar Mountain to the north, by Douglas, Cross, and Juniper Mountains to the south. To the east the formation gradually thins out and is eroded away just before the town of Craig, the present western terminus of the Denver and Salt Lake Railroad ("Moffat Line"), is reached. Four large streams cut through this sedimentary mass: the Green River from the west; Vermillion Creek and Little Snake River from the north; and the Yampa River from the east. All these streams join the Green River before the latter stream reaches the southern flanks of the Uinta and Yampa Mountains. The region in which the fossils were found may be reached by automobile from Craig, Colorado, by way of the small stations Lay, Maybell, and Sunbeam. About two miles to the south of Sunbeam is the first locality in which fossils were found in 1923 by the party from the Carnegie Museum. Some twenty-five or thirty miles west of Sunbeam on Weller's Ranch near Smelter Ranch and Gray Stone Post Office is the locality in which the bulk of our material was collected during the years 1925-26. This locality may be reached by roads from Rock Springs, Wamsutter, or Rawlins, Wyoming, on the Union Pacific Railroad; or from Rifle, Colorado, on the Rio Grande Railroad, or from Vernal, Utah.

## GEOLOGY.

(Pl. IX).

All geologists who have studied the Brown's Park sediments have observed their unconformity with underlying formations. To the west, northwest, southwest,

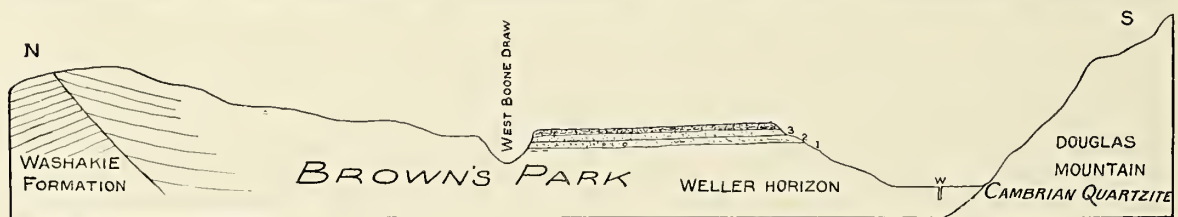


Fig. 1. Cross-section from N. to S. of the Brown's Park sediments at the foot of Douglas Mountain, northward twelve to fifteen miles to the contact with the Washakie formation (Upper Eocene) of the Sandwash Basin. 1, 2, 3, Fossiliferous layers at the top of the Weller horizon. W. Well of water eighty to one hundred feet deep on Weller Ranch.

and south the sedimentary mass rests quite generally on older formations from the Cambrian up to the Mesozoic, which form the flanks of the Cold Spring, the Uinta, the Cross, and the Juniper Mountain uplifts. In places along the southern border,

for example at Danforth Hills, the Brown's Park lies on the upturned edges of the Cretaceous rocks (Mesaverde and Mancos Shales). The eastern and considerable portions of the northern border of the Brown's Park beds form contact with the Cretaceous. Along the northern border where the Brown's Park rests on the "Laramie"<sup>10</sup> the writer found no remains of vertebrates, but found fossil wood in considerable abundance in the latter formation.



Fig. 2. Brown's Park Formation resting on Cretaceous at Danforth Hills, about two miles west of "Bob Hugh's Canyon." At the contact the Brown's Park beds dip to the north about five degrees, gradually changing to horizontal towards the basin. There is no evidence of conglomerate in contact at the base of the Brown's Park Formation in this section.

C. A. White<sup>11</sup> recognized the Brown's Park sediments at Cedar Mountain to the north of Craig. Gale, Sears, and Hancock (*ll. cc.*) indicate these same sediments as an outlier of the main body of the Brown's Park formation. Cedar Mountain is completely surrounded by the Brown's Park sands and sandstone and the elevation itself is covered with basalt, which according to Sears "rests upon white sandstone of the Brown's Park formation." Hancock found some of the Brown's Park sandstone resting upon the basalt.<sup>12</sup> According to these investigations the Brown's Park formation and the basalt formation of Cedar Mountain are of the same geological age which is now determined to be upper Miocene. The Cedar Mountain region was not visited by the writer during his recent trip to western Colorado.

The northern border of the Brown's Park sediments for the greater distance from Cold Spring Mountain to the eastern limit, rests unconformably chiefly on Tertiary beds of the Wasatch, the Green River, and the Washakie (*Cf.* Pl. IX). Continuing eastward the northern border is found resting on the Cretaceous, as already stated. Contact sections were obtained between the Brown's Park and

<sup>10</sup>Gale, H. S. Bull. 415, U. S. Geol. Survey 1910. Note: On page 69 Gale says that "the Laramie formation overlies the Mesaverde in the Yampa coal-field, intervening between the Mesaverde and the succeeding tertiary formations." Gale again discusses the Laramie on pages 72 & 73 of the same work, Sears (Bull. 751 G, U. S. Geol. Surv., 1924, p. 291) apparently follows Gale in referring this formation to the Laramie in their work in Moffat County, Colorado.

<sup>11</sup>Ninth Ann. Report U. S. Geol. Survey, 1889, p. 691.

<sup>12</sup>U. S. Geol. Survey, Prof. paper 90, p. 187, 1915.



underlying beds at points visited by our party, which indicate considerable variations of dip in the Brown's Park sediments in different localities. Sears states<sup>13</sup> that "between the outward-dipping older rocks and the inward-dipping sandstones of the Brown's Park, there is angular unconformity ranging from 10 to 100 degrees."



Fig. 3. Brown's Park Formation resting on Cretaceous, "Post Laramie," northwest of Lay Post Office, Moffat County, Colorado. The dip of the Cretaceous is about 15° and that of the Brown's Park 12°. To the south, or toward the basin, the Brown's Park sediments gradually become horizontal. C. Basal conglomerate of the Brown's Park Formation about seventy feet thick.

In the Brown's Park sediments along the northern border there is a general presence of a basal conglomerate, which varies considerably in vertical depth, and may be of stream-origin. This conglomerate is seldom noticed at contacts to the south. I fully agree with Sears<sup>14</sup> in regarding this basal conglomerate as of the same general age as the Bishop Conglomerate, exposed in many places on either side of the Uinta Mountains, the much greater dip of the Brown's Park strata at its present borders than in the basin proper is due, at least in part, to movements which took place subsequent to the deposition of the Brown's Park beds. Sears says: "as the Brown's Park forms the ridge, and the Eocene beds to the north in Sandwash Basin are at a lower elevation, these escarpments cannot mark the edge of deposition which stopped short of the zone of disturbance. The only possible explanation seems to be that the region to the south was depressed after Brown's Park time, and that the soft Brown's Park beds north of the zone, left at a much higher elevation, have been entirely eroded" (*l. c.* p. 292). The Brown's Park formation must thus be regarded as having formerly covered a territory of great extent, of which now only relatively small remnants are left on either side of the Uinta-Yampa uplifts. White states that "remaining patches of (Uinta sediments) show that the formation formerly extended eastward as far as the foothills of the Park Range."<sup>15</sup>

The Brown's Park sediments, outside of the basal conglomerate, are generally composed of soft, almost chalk-white sands and sandstones cemented with lime, sometimes intercalated with slightly argillaceous bands. This is generally the

<sup>13</sup>Bull. Geol. Soc. of America, Vol. 35, 1924, p. 287; Bull. 751, p. 306, U. S. Geol. Survey, 1924.

<sup>14</sup>Bull. 751-G, U. S. Geol. Survey, 1924, p. 296.

<sup>15</sup>Tenth Ann. Report, U. S. Geol. Surv., 1877, p. 38.



most characteristic feature in the eastern and middle sections of the basin, where the formation weathers into ravines, buttes, and table-lands. The Weller horizon,

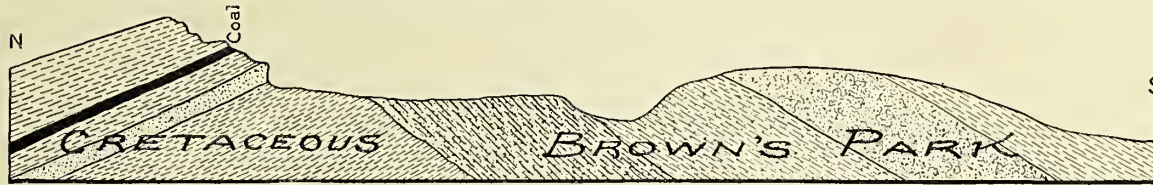


Fig. 4. Section shown five miles north of Sunbeam, Moffat County, Colorado. At this point the Brown's Park Formation is found resting on the Cretaceous at an angle of about  $34^{\circ}$  to the south. There is evidence of cross-bedding, but no basal conglomerate of the Brown's Park sediments was found.

exposed at the northern flanks of the Douglas Mountain, on the Weller ranch near the Gray Stone Post Office, consists of very soft sandstone, which weathers into sandy ridges capped by a layer of harder sandstone from six to fifteen feet thick. This harder sandstone (the Weller Sandstone) presents sufficient resistance to erosive agencies to form broad table-lands, which are usually covered by Pinions



Fig. 5. Type locality of the Weller horizon, at which most of the fossil remains were found on the Weller Ranch. Northern base of Douglas Mountain, looking toward the basin.

and Juniper trees, a characteristic feature throughout the middle section of the Brown's Park basin. A vertical section of about 736 feet, from the Cambrian contact to the top of the Weller sandstone, may be named the Weller horizon. Toward the upper part of this horizon the main bulk of the fossil remains found in Brown's Park by the parties from the Carnegie Museum were obtained. The Weller sandstone is approximately in the middle vertical section of the sedimentary mass of the Brown's Park. The horizon above the sandstone (the Upper Brown's Park)

did not yield fossil remains, although its lithological characters are practically similar to the section below the Weller sandstone. (See fig. 1.)

The western end, or the Green River and Vermillion Creek exposures, often show material of different lithological composition. The color is a light gray, or quite similar to that in the middle and eastern sections, but the wearing down of the formation, especially of this portion along the Vermillion, leaves vertical cliffs of great height. The Brown's Park sediments in this section consist of alternating harder and softer layers of sandstone. The harder layers are heavily charged with lime, often with condensed flint-like or chalcedonous masses of considerable size, or with parts full of cavities ranging from minute size to small caverns, sometimes like geodes. This whole sedimentary mass appears as if it may have had its origin, in part, from numerous warm springs distributed over a large area of the western end of the basin. The deposition from warm springs may account for the local unconformity mentioned in Sears' report (*l. c.* Bull. 751 G. p. 291). Although diligent search for fossil remains was made by the parties from the Carnegie Museum in 1925-26, nothing was found. The shaft of a limb bone was found near Jarvis Ferry on Green River by the writer in 1894, as reported in an earlier publication (*Ann. Car. Mus.*, Vol. XV, 1924 p. 299).

### UINTA BASIN

On the southern flanks of the Uinta Mountains there are a series of soft argillaceous sandstones and arenaceous clays, approximately one thousand two hundred to one thousand four hundred feet thick having a reddish yellow color.<sup>16</sup> In an east and west line these sediments extend from Deadman's Bench east, to the vicinity of Strawberry Valley at the western end of the Uinta Basin. Major Powell and other early observers appear to have associated these uppermost beds of the Uinta Basin with the typical Brown's Park formation to the north and east of the Uinta and Yampa uplifts. Among workers in later years Schultz<sup>17</sup> clearly recognizes the Bishop conglomerate and the overlying Tertiary rocks.

From what is generally regarded as the base of horizon C at "Kennedy's Hole" in the eastern borders of that horizon westward to the vicinity of the Ouray Agency on Green River and Myton on the Duchene River the fauna is known through the researches of Marsh, Osborn, Scott, Hatcher, Douglass, and Peterson. In 1894 and

<sup>16</sup>U. S. Geol. Surv. Terr., Fourth Ann. Report 1870, p. 57; U. S. Geol. Surv. Terr., "Geology of the Uinta Mountains", 1876, p. 168; U. S. Geol. Surv., Tenth Ann. Report, 1877, pp. 18, 19; Report Exploration 40th Paral., Vol. II, 1877, p. 225.

<sup>17</sup>Schultz, Alfred R., U. S. Geol. Surv., Bull. 690-C, 1918, pp. 56, 67, 86 and map of the Phosphate Deposits along the north and south slopes of the Uinta Mountains in Northeast Utah.



succeeding years Peterson<sup>18</sup> while collecting fossils in the Uinta basin found it convenient to divide the Tertiary strata overlaying the Green River formation into three horizons, A, B, and C. The Brown's Park Beds were recognized, but it is now quite evident that this formation, or horizon C, was regarded as extending too far down into the upper Eocene sediments, or into the horizon B of the Uinta. This error was due to the fact that no distinct break between the Eocene and the Brown's Park beds were found by Peterson in 1894. Riggs<sup>19</sup> in 1912 wrote quite complete stratigraphic notes and furnished sections of horizons A and B of the Uinta sediments, but did not take up any discussion of horizon C, because he apparently did not collect any fossils in these clays and fine-grained sandstones. According to field notes Peterson in 1912 continued a search, without success, for a true contact between the Uinta and Brown's Park along the southern borders of the latter formation. At the southern base of the Uinta Mountains Brown's Park rests unconformably on all underlying formations from the Green River Tertiary<sup>20</sup> to the Cambrian, while along the southern edge of the formation, due to unusual conditions, Brown's Park rests upon a Uinta or upper Eocene sedimentary surface comparatively undisturbed.

It seems most advisable to retain horizon C in our records, but to restrict the horizon to those clays and sandstones in which *Diplacodon*, *Protitanotherium*, *Eotitanotherium* and most of the microfauna of the Uinta sediments were found by the earlier and later collectors. This horizon would then include the softer sandstones, the fine grained sandstones and clays above horizon B, from Kennedy's Hole in the eastern end of the Uinta basin westward to Chipita Grove on White River, thence westward to the Ouray Agency and up Duchene River to Myton. The ultimate discovery of contact between the proposed horizon C and the true Brown's Park will then govern the vertical thickness of both horizon C and the overlying Brown's Park. It is quite obvious, that, if we accept, as seems logical, the determination by many geologists, including the latest work by Schultz<sup>21</sup> that the Bishop conglomerate along the southern flanks of the Uinta Mountains underly Tertiary beds we cannot regard these as upper Eocene or lower Oligocene in the Uinta Basin while to the north and east of the mountains these beds, the

<sup>18</sup>Peterson, O. A., Bull. Amer. Mus. Nat. Hist., Vol. VII, 1895.

<sup>19</sup>Riggs, E. S., Field Mus. Nat. Hist., Pub. 159, Geol. Series, Vol. IV, 1912, pp. 17-25.

<sup>20</sup>The typical horizons A and B of the Uinta sediments are not exposed below the Brown's Park along the northern border of the latter formation.

<sup>21</sup>Schultz, A. R., See map and pages cited above.



Bishop conglomerate and Brown's Park, are now known to be late Miocene.<sup>22</sup> Secondly, by retaining horizon C of the Uinta Eocene we would keep undisturbed our published records of paleontology.

### PLEISTOCENE

Occasionally there are thin deposits of Pleistocene age along small stream valleys in the Brown's Park basin. On Lay Creek there is found such a deposit made up of worked over material of the Brown's Park and underlying formations. A molar tooth of a Pleistocene proboscidean was found quite close to the Lay Post Office on Lay Creek which is figured in this report.

### THE FAUNA OF THE BROWN'S PARK FORMATION

Class **MAMMALIA**

Order **CARNIVORA**

Family **PROCYONIDÆ**

Genus **BASSARISCOPS** nov.

*Type:* *Bassariscops willistoni* (Peterson).

*Phlaocyon willistoni* Peterson. (Cf. Annals Carnegie Museum, Vol. XV, 1924, p. 300). Anterior portion of skull, C. M. Cat. Vert. Fossils, No. 11,332; right ramus of the lower jaws, C. M. Cat. Vert. Fossils, No. 11,333; and the left lower jaw No. 11,334 provisionally referred.

*Locality:* One mile south and west of Sunbeam, Moffat County, Colorado.

*Horizon:* Brown's Park Formation, Weller horizon.

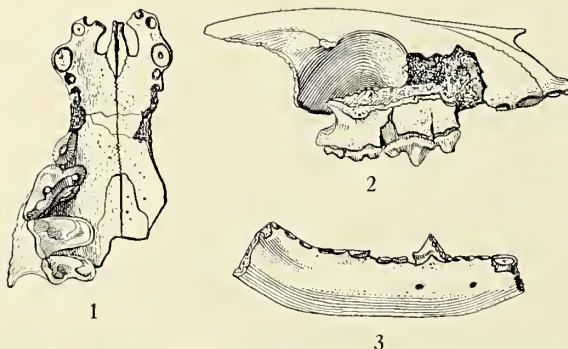


Fig. 6. *Bassariscops willistoni* (Type, C. M. Cat. Vert. Foss. No. 11,332) 1, Palatal view; 2, lateral view; 3, lateral view of lower jaw (C. M. Cat. Vert. Foss. No. 11,333). All figures natural size. (Reproduced from Ann. C. M., XV, p. 301).

<sup>22</sup>Very recently there has come to the hands of the writer two specimens just discovered in the Brown's Park of the Uinta Basin which will help us in the determination of the geological age of "horizon C," or the true Brown's Park formation south of the Uinta Mountains. The description of these specimens appears in the sequel.

A very thorough comparison recently made between the types of *Phlaocyon lecosteus* Matthew and *Phlaocyon willistoni* Peterson convinces me that the latter specimen is not referable to *Phlaocyon*. The specimen from the Brown's Park formation, though later in time than *P. lecosteus*, is in some respects less advanced than *P. lecosteus* and apparently more nearly in the line of a *Bassariscus*-like animal. Thus, while the muzzle is broad as in *P. lecosteus*, nasals, infraorbital foramen, canine and the trigon of the carnassial similar; the premolar crowns are more compressed laterally, with greater basal areas in front and back; the shearing blade of the carnassial more distinctly separated from the median, or main cusp.<sup>23</sup> The sectorial tooth is, as originally stated by Peterson, relatively longer than in *Phlaocyon lecosteus*. The molars, especially the second, are also broader than in the genus *Phlaocyon*.

In the original description the specimen from Brown's Park was said to be equal in size to *Bassariscus*. The muzzle is broader than in the latter, but the cheek-teeth, though relatively larger, are quite similar, the antero-internal tubercle of P<sup>4</sup> of course further forward than in the recent genus from the southwestern United States.<sup>24</sup> The new genus stands close to *Phlaocyon*, but, as stated, more nearly in line with *Bassariscus*.

The ramus of the lower jaws, No. 11,333, referred to this species, is of the same size, slenderness, and curvature as that in *Bassariscus*. Unfortunately the teeth are represented for the most part by roots only, but I am able to determine that the

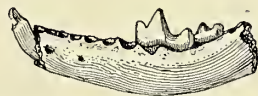


Fig. 7. *Bassariscops willistoni*. External view of lower jaw (C. M. Cat. Vert. Foss., No. 11,334) natural size. (Reproduced from Ann. C. M., XV, p. 303)

canine is large, the crowns of the premolars compressed laterally as in *Bassariscus*, and, though there was a M<sub>3</sub> present, this tooth was undoubtedly quite rudimentary.

<sup>23</sup>In my original description, Ann. Car. Mus. Vol. XV, p. 301, I erroneously concluded that the apparent separation of the sectorial tubercle from the protocone is due in great extent to wear.

<sup>24</sup>Very recently there has come into the hands of the writer a paper by E. Raymond Hall (Univ. of Cal. Press, Vol. 16, No. 11, March 17, 1927) in which he speaks (p. 442) of certain Pleistocene remains of the *Bassariscinae* from the Potter Creek Cave, Shasta County, California. On plate 64, fig. *g*, of this work Hall furnishes a photographic reproduction of the left maxilla with P<sup>4</sup> and the molars in position. The protocone of P<sup>4</sup> has the forward position as in *Bassariscops* and *Phlaocyon* described by Matthew and as in the early *Canidae* generally. The postero-internal tubercle on P<sup>4</sup> of the Potter Creek Cave specimen is apparently larger than in *B. willistoni*; the tooth has a slightly less antero-posterior diameter, and there appears to be a minute tubercle on the basal cingulum opposite the sectorial blade which is absent on the cingulum in the Brown's Park specimen. Altogether it appears that the California specimen may be closely related to the Colorado species and perhaps should not be regarded as a true *Bassariscus*.



The left lower jaw, No. 11,334, referred to this species is of considerably smaller size than the jaw with the type. This specimen was doubtfully referred to *Phlaocyon* by Peterson, *l. c.*, p. 303. At present I am convinced that the difference in size of the two specimens (Nos. 11,333-11,334) under study could easily be individual or sexual. The three specimens (type and paratypes) were found together. The outlines and detailed structure of the ramus, as well as evidence of  $M_3$  in the two specimens, Nos. 11,333 and 11,334, are quite identical. The carnassial tooth of No. 11,334 from the Brown's Park beds, while apparently having the same antero-posterior diameter as that tooth in *Probassariscus antiquus*,<sup>25</sup> is slightly narrower, higher, and sharper;  $M_2$  is smaller and the postero-internal angle distinctly less developed. This, together with the absence of a paraconid ridge, which is present in both *Probassariscus antiquus matthei*<sup>26</sup> and *P. antiquus*, would seem at least for the present to prevent the association of the specimens from Brown's Park with *Probassariscus*.

*Principal Generic Characters Shown by the Type.* Broad muzzle; trigon of  $P^4$  triangular as in *Phlaocyon* including the presence of the postero-internal cusp; premolars in front of carnassial compressed more nearly as in the cynoids; sectorial tubercle of  $P^4$  long and separated from the protocone by a deep excavation on the buccal face of the tooth; upper molars relatively broad when compared with *Phlaocyon*. The associated mandibular rami, so far as comparison permits, are closely similar to those of *Bassariscus astuta*. The molars are also quite like those in the recent species, except a smaller and less perfectly developed heel on  $M_2$  and the presence of the rudimentary  $M_3$ .

The relationship between *Bassariscus* and *Bassariscops*, as revealed by the type and material associated with the latter, is most remarkably close. The lower jaws of the fossil and recent forms are identical, so far as one can judge from the available material. The cheek-teeth occupy the same relative area in the jaws of the two except that  $M_3$  is present in the fossil form. In the skull of *Bassariscops*, on the other hand, we have a broad muzzle (presumably also a broad symphysis of the lower jaws) and  $P^4$  with a primitive trigon.

With the recession of the antero-internal tubercle, the slight enlargement of the postero-internal tubercle of  $P^4$  and the reduction of the muzzle we would have, so far as the fragmentary type reveals, a very close relative of *Bassariscus*.<sup>27</sup>

<sup>25</sup>Bull. Amer. Mus. Nat. Hist., Vol. XXVI, 1909, p. 377.

<sup>26</sup>Univ. Cal. Publications, Vol. VI, 1911, p. 246.

<sup>27</sup>Perhaps even a closer relative to the recent form than *Bassariscus parvus* from the Upper Miocene, Stewart Valley, Nevada, recently named by Hall, Univ. Calif. Publications, Vol. 16, 1927, p. 440.



Order **ARTIODACTYLA**  
 Family **OREODONTIDÆ**<sup>23</sup>  
 Genus **TICHOLEPTUS** (?)

A fragment of a left lower jaw with  $P_4$  and  $M_1$  in position, which has recently come into the hands of the writer, is referred to these American primitive ruminants. The specimen is reported by Mr. Wm. Haslem of Vernal Valley, Utah, to have been found on top of a butte close to the camp of the Emma (Gilsonite) Mine near the bluff of the White River canyon in Utah. If this is the locality at which this specimen was found<sup>29</sup> we have perhaps at last located the contact between the true Brown's Park formation and the horizons A, B, and C of the upper Eocene sediments in the Uinta Basin.



Fig. 8. *Ticholeptus*?; fragment of mandible with premolar in place (C. M. Cat. Vert. Foss., No. 11,391) natural size.

In size the specimen referred to compares with the larger species of *Ticholeptus* (*T. breviceps* Douglass and *T. petersoni* Loomis), but may perhaps be from a later geologic horizon than either. The detailed structure of  $P_4$  in the specimen from the Uinta Brown's Park is almost identical with that in *Ticholeptus breviceps*. The latter species has, however, a well marked basal cingulum, which is entirely wanting in the specimen from Utah. The excavation of the external face of  $P_4$ , which gives a laterally constricted appearance to the mid-anteroposterior region of the crown in *T. breviceps*, is very much less pronounced in the specimen from Utah. Altogether the latter specimen appears possibly to be of a later geologic age than the species from Montana.  $M_1$  is much worn and displays the usual features found in well worn teeth of the oreodonts. The specimen has been presented to the Carnegie Museum and bears Catalog No. 11,391.

<sup>23</sup>Leidy, Extinct Mammalia of Dakota and Nebraska, Journal Acad. Nat. Sci. Phila., Vol. VII, 1869, p. 71.

<sup>29</sup>There does not now seem to be any reason for doubt as to the accuracy of Mr. Haslem's report.

## Family TYLOPODA.

Genera? Species?

(Plate X. figs. 3, 4).

In the Weller horizon of the Brown's Park sediments were found the distal end of the humerus and the greater portion of the radius and ulna of a Cameloid about the size of *Oxydactylus longirostris* from the Miocene of western Nebraska.<sup>30</sup> Perhaps the most noteworthy feature in what is left of the humerus is the very feeble development, or rather absence, of the crista on the capitellum of the distal articulation of the bone. In *Oxydactylus longirostris* the crista, or intertrochlear ridge on the capitellum, is distinctly more developed than in the type of the genus, *O. longipes*. A second feature of the specimen under description is the perforation of the bony septum at the bottom of the olecranon fossa, through which protrudes the point of the process on the lower edge of the olecranon of the ulna on extreme flexion of the elbow joint. It is quite evident that the camel represented by the specimen here described cannot be placed with the genus *Oxydactylus* and is provisionally regarded as a cameloid of a later geological horizon.

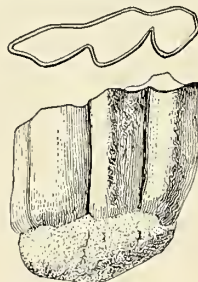


Fig. 9. Cameloid allied to *Stenomylus*; M<sub>3</sub> of right side (C. M. Cat. Vert. Foss., No. 11,336) natural size. (Reproduced from Ann. C. M. XV, p. 304)

A smaller cameloid is represented by the tibial half of an astragalus and a fragment of a phalanx. In size the animal to which these parts belong was between *Oxydactylus longiceps* and *Stenomylus gracilis*, but nearer the latter. Both the astragalus and phalanx are typical of the Miocene Tylopoda. To this is also doubtfully referred a fragment of a tympanic bulla. The molar tooth (See fig. 9) described and figured in an earlier paper may also be provisionally placed here.<sup>31</sup>

## SUBORDER BOOIDEA

Family MERYCODONTIDÆ Matthew.

Genus MERYCODUS? sp.?

In extracting the remains of *Serridentinus fricki* (See *infra*) from the matrix

<sup>30</sup>Ann. Car. Mus. Vol. VII, 1911, p. 260.

<sup>31</sup>Ann. Car. Mus. Vol. XV, 1924, p. 304.



there were found commingled with these remains the greater portion of a scapula and fragments of the phalanges of a *Cervid* (C. M. Cat. Vert. Foss., No. 11,385), which compare fairly well with these parts of *Merycodus* from the Middle Miocene of other localities. No generic or specific determination can be made.

Order **PERISSODACTYLA**

Family **RHINOCEROTIDÆ**

Genus **APHALOPS**

*Aphalops ceratorhinus* Douglass<sup>32</sup>

(Plate X, fig. 1, 2, and 5)

Vertebræ, ribs, limb-bones, and the greater part of the left foot of one individual of a large rhinoceros were found in the upper part of the Weller horizon of the Brown's Park formation. The calcaneum of the type (of which Douglass gives the fibular view in his paper of 1908) is identical in size and general structure, with that bone in the hind foot from Brown's Park. After a critical comparative examination, so far as the material permits, there is little or no hesitation on the part of the writer in referring the remains from Brown's Park to *Aphalops ceratorhinus*.

For the purpose of a better appreciation of the anatomical differences between the well known *Teleoceras fossiger* and the little known *Aphalops ceratorhinus* a comparative description will here be given. On plates IV and V in the Bulletin of the American Museum of Natural History, Vol. XXXVIII, Dr. W. D. Matthew illustrates the fore and hind feet of *Aphalops ceratorhinus* (No. 9745, A. M. N. H. Catalog), from the Madison Valley beds of Montana. Matthew regards this specimen as a topotype of the species, but furnishes no detailed description of the specimen, except very briefly on p. 206 of the same publication.

THE VERTEBRAL COLUMN

The vertebral column is represented by the last dorsal, three lumbar, and two posterior centra of the sacrum. Centra of the posterior dorsals and the lumbar are in general construction similar to those in *Teleoceras*, but the neural spines relatively greater in their antero-posterior diameters. The summit of the third lumbar vertebra is much reduced in its antero-posterior diameter, when compared with those in front of it. The centra of the sacrum are distinctly more delicate in their proportion than the corresponding parts in *Teleoceras*.

<sup>32</sup>Douglass, Earl, Ann. Car. Mus., Vol. II, 1903, p. 195; *ibid.* Vol. IV, 1908, p. 260.



## RIBS

The ribs are represented by numerous fragments from different parts of the thorax. Shafts of the third (?) fourth (?) and a great number of the posterior ribs are among the best parts preserved. The shafts of the first ribs appear to be slenderer than in *Teleoceras*. In fact all the ribs, judging from the material in hand, are lighter in construction than in the latter genus, and no doubt the thoracic cavity was smaller in *Aphalops ceratorhinus*.

## MEASUREMENTS

Last dorsal and three lumbar vertebra: total length of series.....	300 mm.
Last dorsal vertebra: length of centrum.....	83 mm.
Last dorsal vertebra: height of spine.....	103 mm.
Last dorsal vertebra: antero-posterior diameter of neural spine, near top.....	73 mm.
First lumbar vertebra: length of centrum, approximate.....	74 mm.
First lumbar vertebra: antero-posterior diameter of neural spine, near top.....	74 mm.
Second lumbar vertebra: length of centrum approximate.....	80 mm.
Second lumbar vertebra: antero-posterior diameter of neural spine, near top.....	74 mm.
Third lumbar vertebra: length of centrum, approximate.....	77 mm.

## FORE LIMB

(Plate X, fig. 2)

The scapula of *A. ceratorhinus* is long, narrow, and rather delicately formed, when compared with the same bone in *Teleoceras fossiger*. The spine and subscapular border rise more gently from the glenoid cavity upward and the coracoid is decidedly less developed than in *A. fossiger*. In the specimen from Brown's Park the suprascapular border is slightly injured, but enough is preserved to determine that this border is more nearly rounded and does not terminate above in the prominent tubercle characteristic of *Teleoceras fossiger*. The spine overhangs the subscapular surface in a similar manner as in *A. fossiger*, but it terminates in a much less developed tubercle than in the latter species. The glenoid cavity is entirely wanting in the specimen under description.

## MEASUREMENTS

Scapula, from coracoid border to suprascapular border.....	500 mm.
Scapula, greatest antero-posterior diameter of blade.....	200 mm.
Scapula, antero-posterior diameter of scapula just above glenoid cavity.....	115 mm.

## FORE FOOT

In the specimen under description Mc.II is slenderer than in *A. fossiger*. This is especially noticeable when the proximal and distal ends of these bones in the two

species are compared. In *A. fossiger* the diameter, especially of the proximal end, is as great as, or greater than, in *A. ceratorhinus*, while the length of the bone is over thirty millimeters shorter than in the latter. The shaft of Mc.II in *A. fossiger* is accordingly seen to be much constricted when compared with the same bone in the specimen being described. While the dorsal face of Mc.II is similar in the two species compared, the palmar surfaces differ. In *A. ceratorhinus* there is a median keel-like ridge, especially well developed halfway between the proximal and distal ends. This ridge divides in equal proportions the internal and external parts of the shaft, while in *Teleoceras fossiger* the median ridge is absent, and instead there is a heavy osseous development along the entire length of the shaft near the radial border. External to this ridge, especially in fully adult and old individuals of *T. fossiger*, there is developed a deep fossa taking up the greater area of the palmar face, while in *A. ceratorhinus* the palmar face of Mc.II has a fossa on either side of the median keel. In the latter species there are deep pits on either side of the shaft near the distal articulation; the pit externally is especially large and deep. In *T. fossiger* these pits for muscular attachments are quite generally absent; when present, they are much less developed. There are no noteworthy differences in the distal and proximal articulations of Mc.II in the two genera.

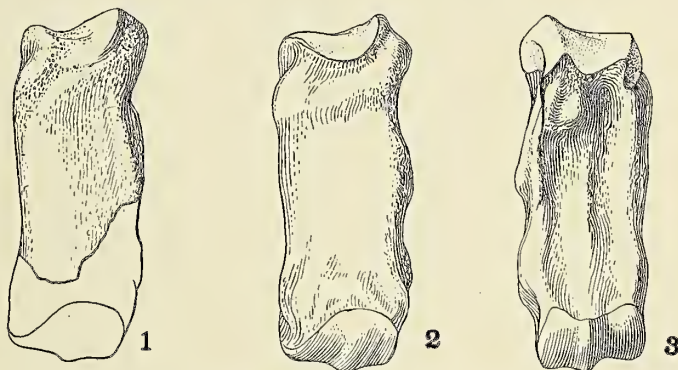


Fig. 10. *Aphalops ceratorhinus* Douglass. 1, Dorsal view of Mc.II, type specimen (C. M. Cat. Vert. Foss., No. 857); 2, *A. ceratorhinus*. Dorsal view of Mc.II, (C. M. Cat. Vert. Foss., No. 11,387); 3. Palmar view of Mc.II, (C. M. Cat. Vert. Foss. No. 11,387). All figures one-third natural size.

The proximal end and a considerable portion of the shaft of Mc. II is present in the type of *A. ceratorhinus*. These parts agree quite well with the characters in the specimen from the Brown's Park beds just described.

The proximal phalanx of the second digit is short and heavy and in a general way similar to that in *Teleoceras*. The ungual phalanges, which we possess, are longer and not so broad as in the latter genus.



## MEASUREMENTS

Mc. II: greatest length.....	138 mm.
Mc. II: greatest transverse diameter of head.....	54 mm.
Mc. II: greatest antero-posterior diameter of head.....	36 mm.
Mc. II: greatest transverse diameter of shaft.....	53 mm.
Mc. II: greatest transverse diameter of distal trochlea.....	44 mm.
Mc. II: greatest antero-posterior diameter of distal trochlea.....	39 mm.

## HIND LIMB

The pelvis is represented by fragments of the ilia. This part of the hind limb appears to be a broad flaring gluteal surface and a short posterior shaft, perhaps not unlike that of *Teleoceras*.

## FEMUR

(Pl. X, figs. 1 and 5)

The femur of *Aphalops ceratorhinus* is at once distinguished from that of *Teleoceras fossiger* by the extraordinary development of the lesser trochanter. The bone is flattened by crushing, which somewhat exaggerates the size of the lesser trochanter, but, allowing for the crushing, the tubercle is of extra large size and otherwise quite like that in *Rhinoceros bicornis*. The articulating head sits low on the proximal end and the superior portion of the great trochanter is on nearly an even transverse line with the articulating head, in part perhaps due to crushing, while in *T. fossiger* the trochanter is placed lower. The third trochanter agrees more in its proportion with that in *T. fossiger*. The shaft is slenderer than that of *T. fossiger*. The tuberosities for the internal and external lateral ligaments are more prominent than in *T. fossiger*. The borders of the rotular trochlea are nearly equally developed, while in *T. fossiger* the internal trochlea is much the larger. The subequalness of the internal and external borders of the rotular trochlea in the specimen under study is no doubt due in part to crushing, but, as in the case of the lesser trochanter just described, when due allowance is made for distortion, the internal border is unusually small for a rhinoceros, and more in line with the titanotheres and *Moropus*.

## TIBIA AND FIBULA

With the exception of a few fragments of the distal end, the tibia and fibula are broken up into fragments too minute for detailed study. The posterior portion of the facet for the astragalus displays no noteworthy differences from the corresponding part in *Teleoceras*, while the distal end of the fibula is more delicate in construction than in the latter genus, and compares better with such forms as *Diceratherium*.



## MEASUREMENTS

Femur: Greatest length.....	546 mm.
Femur: Transverse diameter at proximal end.....	230 mm. <sup>33</sup>
Femur: Transverse diameter at tuberosity for lateral ligament.....	170 mm. <sup>33</sup>
Femur: Transverse diameter at articulation with the tibia.....	142 mm. <sup>33</sup>

## ASTRAGALUS

The trochlea for the reception of the tibia is deeper in the astragalus of *A. ceratorhinus* than in *T. fossiger*. Distally the articulation for the navicular is more

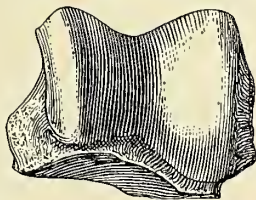


Fig. 11. *Aphalops ceratorhinus* Douglass. Dorsal view of astragalus, (C. M. Cat. Vert. Foss., No. 11,387) one-third natural size.

oblique and convex and the articulation for the cuboid is smaller than in *Teleoceras fossiger*. The facets for the calcaneum are perfectly convex and concave as in *Rhinoceros bicornis* and thus form a more perfect interlocking joint than in *Teleoceras fossiger*. With the exception of a longer neck between the distal and proximal articulations of the astragalus in the Black Rhinoceros this bone in the latter and the fossil form under description are very similar.

## CALCANEUM

The most conspicuous differences in the calcanea of *Aphalops ceratorhinus* and

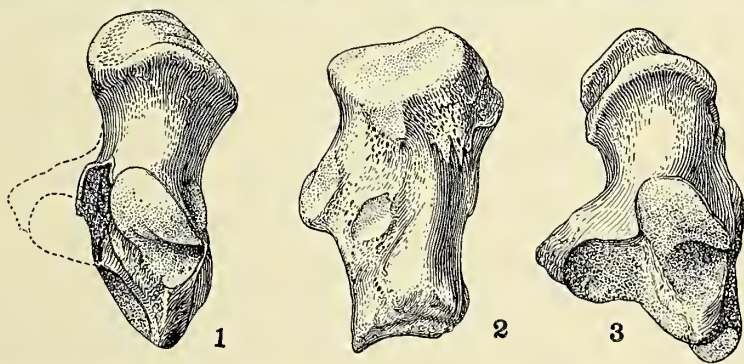


Fig. 12. *Aphalops ceratorhinus* Douglass. 1 and 2, Dorsal and plantar views of calcaneum (type) (C. M. Cat. Vert. Foss., No. 857); 3. Dorsal view of calcaneum (C. M. Cat. Vert. Foss., No. 11,387). All figures one-third natural size.

*Teleoceras fossiger* are the relatively longer *tuber calcis* and broader articulation for the astragalus in *Teleoceras*. The facets for the astragalus correspond perfectly to those on the astragalus just described. The short and heavy *tuber calcis* and

<sup>33</sup>Measurement not reliable due to crushing of the bone.

many other features in the calcaneum of the recent species from Africa are similar to those in *Aphalops ceratorhinus*, but in the recent form the articulating trochlea for the tibia is continued from the astragalus back upon the calcaneum to form a small facet at the base of the tuber calcis and distally the greater and lesser processes are separated by a deep tendinal groove not observed in the fossil.

## CUBOID

Great dissimilarity in the cuboid of *A. ceratorhinus* and *T. fossiger* is found in the shape and position of the plantar process. In the latter species the plantar

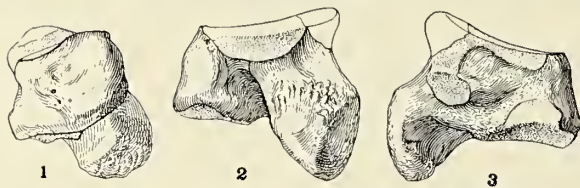


Fig. 13. *Aphalops ceratorhinus* Douglass. Cuboid (C. M. Cat. Vert. Foss., No. 11,387) one-third natural size. 1, Dorsal view; 2, Tibial view; 3, Fibular view.

process is as large as that of the articulating body of the bone in front of the process; the process is cubical in shape and directed horizontally backward from the main body. In *A. ceratorhinus*, on the other hand, the plantar process is much the smaller portion of the cuboid; it has the usual hook-shaped form met with in the Rhinocerotidæ, thus extending well below the distal articulating surface for Mt. IV, and the bone as a whole has relatively great vertical diameter. Among other noteworthy differences of the cuboid in the two genera, which are being compared, mention may be made of the comparatively downward slanting facet for the calcaneum, which forms a blunt wedge on the tibial face of the cuboid in *Teleoceras*, while in *Aphalops ceratorhinus* the tibial and fibular faces of the bone have practically equal vertical diameters.

## NAVICULAR

The navicular of *A. ceratorhinus* is relatively long and narrow, when compared with that of *Teleoceras fossiger*. As a result of this difference the articulation for

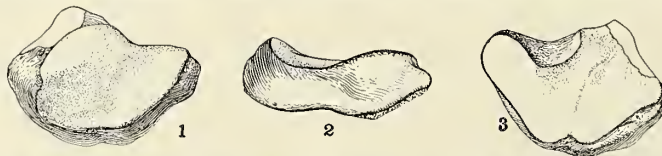


Fig. 14. *Aphalops ceratorhinus* Douglass. Navicular (C. M. Cat. Vert. Foss., No. 11,387) one-third natural size. 1, Proximal view; 2, Dorsal view; 3, Distal view.

the astragalus in the latter genus is simply concave fore-and-aft and slightly convex from side to side, while in *A. ceratorhinus* this articulating surface, besides the con-



cave antero-posterior and convex transverse condition, is oblique or twisted from the dorsal fibular angle to the plantar tibial extremity. The articulation for the cuneiforms differs in the two genera. In *T. fossiger* the triangular-shaped surface for the ectocuneiform is constricted from the oval-shaped surface for the mesocuneiform by excavations in front and back. In *A. ceratorhinus* the two articulating surfaces referred to are not separated, or constricted by anterior or posterior excavations, but the articulation for the ectocuneiform has a much greater invagination from the fibular surface of the bone than is the case in *Teleoceras*. In the latter the facet for the entocuneiform is quite minute and confined to the plantar-tibial angle, while in *A. ceratorhinus* this surface is large and like that for the ecto- and mesocuneiforms, it is located more directly on the distal face of the navicular.

## ECTOCUNEIFORM

The more important differences in the ectocuneiform of *Aphalops* and *Teleoceras* are: the greater backward extension of the facets for Mt. II and Mt. III, and the

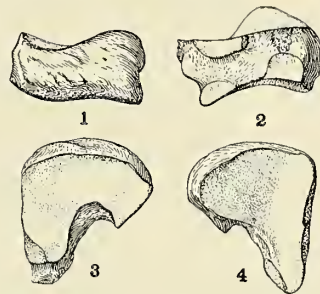


Fig. 15. *Aphalops ceratorhinus* Douglass. Ectocuneiform (C. M. Cat. Vert. Foss., No. 11,387) one-third natural size. 1, Dorsal view; 2, Fibular view; 3, Distal view; 4, Proximal view.

interrupted condition and the position of the facets for Mt. II in *A. ceratorhinus*. In *T. fossiger* the facet for the second digit is continuous from the dorsal to the plantar faces and is at a lesser angle from the facet for Mt. III; while in *A. ceratorhinus* this surface is divided into two facets, located more nearly on the tibial face of the bone.

## MESOCUNEIFORM

The mesocuneiform in the two genera, which are being compared, differ chiefly in the greater width and relative shortness of that bone in *Teleoceras fossiger*.

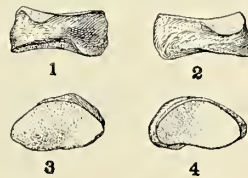


Fig. 16. *Aphalops ceratorhinus* Douglass. Mesocuneiform (C. M. Cat. Vert. Foss., No. 11,387) one-third natural size. 1, Fibular view; 2, Tibial view; 3, Distal view; 4, Proximal view.



## ENTOCUNEIFORM

Next to the calcaneum and cuboid the entocuneiform in the two fossil genera, which are being studied, differs more than any other bone in the pes. In *A. ceratorhinus*



Fig. 17. *Aphalops ceratorhinus* Douglass. Entocuneiform, (C. M. Cat. Vert. Foss., No. 11,387) one-third natural size. Tibial view.

*rhinus* the entocuneiform is of the usual rhinocerotie type, *i. e.* relatively large in size, with great vertical diameter, and with perfectly formed proximal and lateral facets for the articulation of the navicular, mesocuneiform, and Mt.II. In *Teleoceras fossiger*, on the other hand, the bone is reduced, especially in its vertical diameter, and the facet for Mt.II is lost.

## METATARSALS

The chief difference in the metatarsals in the two fossil genera above compared is the relative broadness and shortness of the metatarsals in *Teleoceras fossiger*.

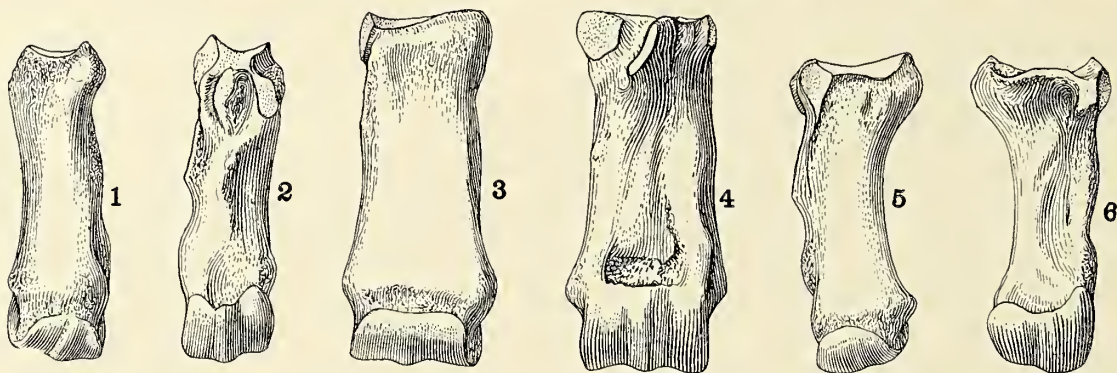


Fig. 18. *Aphalops ceratorhinus* Douglass. 1 and 2, dorsal and plantar views of Mt. II, (C. M. Cat. Vert. Foss., No. 11,387); 3 and 4, Dorsal and plantar views of Mt. III; 5 and 6, dorsal and plantar views of Mt. IV. All figures one-third natural size.

Of perhaps lesser importance is the articular face for the entocuneiform on the tibial face of Mt. II in *A. ceratorhinus*, which is absent in *Teleoceras fossiger*; the subtriangular outline of the articulating face for the mesocuneiform in the latter species; and the lunate outline in *A. ceratorhinus*. The carina on the distal articulation of the metapodials in *A. ceratorhinus* is distinctly more developed than is the

case in *Teleoceras*. This, together with many of the features of *A. ceratorhinus*, which have been above noted, are apparently those of an animal, which lived under conditions not unlike those surrounding the rhinoceroses of today. *Teleoceras fossiger* on the other hand, with its enormous thoracic cavity, its short legs, and the rather simple articular facets of the foot, was, no doubt, an animal rather slow and limited in its movements on land.

## MEASUREMENTS

Astragalus: greatest antero-posterior diameter.....	75 mm.
Astragalus: greatest transverse diameter.....	95 mm.
Calcaneum: greatest length.....	118 mm.
Calcaneum: greatest transverse diameter at sustentacular facet.....	80 mm.
Cuboid: vertical diameter at dorsal face.....	35 mm.
Cuboid: transverse diameter at dorsal face.....	44 mm.
Cuboid: vertical diameter at plantar face including plantar tuberosity.....	64 mm.
Navicular: vertical diameter at mid-dorsal region.....	21 mm.
Navicular: greatest transverse diameter.....	70 mm.
Navicular: greatest antero-posterior diameter.....	48 mm.
Ectocuneiform: greatest antero-posterior diameter.....	56 mm.
Ectocuneiform: greatest transverse diameter.....	45 mm.
Ectocuneiform: vertical diameter at mid-dorsal region.....	21 mm.
Mesocuneiform: vertical diameter at dorsal face.....	16 mm.
Mesocuneiform: transverse diameter.....	20 mm.
Mesocuneiform: antero-posterior diameter.....	36 mm.
Ectocuneiform: greatest vertical diameter.....	62 mm.
Mt: II: greatest length.....	122 mm.
Mt: III: greatest length.....	138 mm.
Mt: IV: greatest length.....	121 mm.

## PHALANGES

The phalanges of *A. ceratorhinus* are represented by a single proximal and two terminals. The proximal phalanx of the second digit is relatively shorter than is

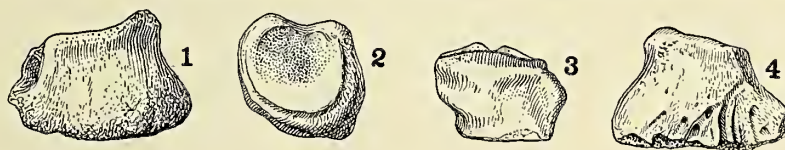


Fig. 19. *Aphalops ceratorhinus* Douglass. 1 and 4, dorsal views of terminal phalanges (C. M. Cat. Vert Foss., No. 11,387); 2 and 3, proximal and dorsal views of proximal phalanx of second digit (C. M. Cat. Vert. Foss., No. 11,387). All figures one-third natural size.

the case in *Teleoceras*. The terminal phalanges on the second and fifth digits are heavy, as in *Teleoceras*, but not nearly so broad.



## Family CHALICOTHEROIDEA

Late in the season of 1926 Mr. LeRoy Kay discovered, near the northern edge of the Brown's Park Formation in the Uinta Basin, Utah, a series of crowns of lower teeth which are referable to the aberrant perissodactyls, the Chalicotheres. This specimen, (C. M. Cat. Vert. Foss., No. 11,392) was discovered approximately in the middle of the vertical section of the sedimentary mass referred to the Brown's Park Formation. The specimen is of unusual interest, because it is among the first recorded specimens from the true Brown's Park Formation south of the Uinta Mountains, and greatly assists in the determination of the geological age of this sedimentary mass.

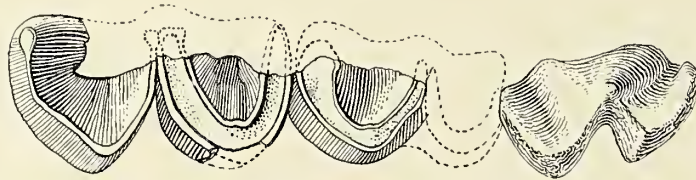


Fig. 20. *Chalicotheroid* Crown view of unerupted  $P_4$ , molars one and two of right lower jaw (C. M. Cat. Vert. Foss., No. 11,392). Natural size.

As stated, the specimen consists of the crowns of an unerupted  $P_4$ , the posterior crescent of  $M_1$ ,  $M_2$ , and fragments indicating upper teeth of a *Moropus*-like animal. In comparing these teeth with *Moropus elatus* from the Miocene of Nebraska the portion of the tooth  $P_4$ , where the anterior and posterior crescents meet, is not nearly as high as in the Nebraskan species. The anterior crescent is more completely filled out, and does not slant nearly so much from before backward, as in *M. elatus*. The first and second molars are badly preserved, but enough is present to determine their moropoid features. Externally the crescents of  $M_1$  and  $M_2$  are fairly well preserved, while internally the crowns were partly weathered away when the specimen was found. In this Uinta form I judge that the crescents of unworn teeth may be filled out to a greater degree, being broader across, than in the Miocene species from Nebraska. It is also of considerably smaller size than the latter. Otherwise there does not seem to be any noteworthy differences between the eastern and western forms, so far as the material permits of comparison.

## Order PROBOSCIDEA

An extraordinary number of genera and species of fossil Proboscidea have been described since the publication of the *Fauna Antiqua Sivalensis*, by Falconer and Cautley (1846). When we shall more completely know the different species, many of which have been founded upon fragmentary types, we probably shall reach a



more satisfactory adjustment of the taxonomy than at present prevails. In the meanwhile it is important to describe and illustrate additional material, especially such as is so complete as that recently discovered by the Carnegie Museum in the Brown's Park beds.

Without attempting to enter upon the discussion of the classification of the fossil Proboscidea, which appears to be in a more or less chaotic state, and in which strongly opposite opinions are maintained by certain authorities as to the validity, or non-validity of some generic names,<sup>34</sup> I have resolved to provisionally refer the specimen hereinafter described to the genus *Serridentinus* erected by Professor Henry Fairfield Osborn, which is the type of the subfamily *Serradentinae*,<sup>35</sup> placed by him in the family *Bunomastodontidae* with the *Longirostrinae* and other subfamilies which have been defined.

GENUS *SERRIDENTINUS* Osborn.

*Serridentinus fricki*<sup>36</sup> sp. nov.

(Plates XI-XV)

*Type*: Greater portion of skull and lower jaws found interlocked in normal position; fragments of vertebræ; ribs and limb bones of an adult, but not old, individual, No. 11,379, C. M. Cat. Vert. Foss.

*Horizon*: Brown's Park Formation, Weller horizon,<sup>37</sup> Middle to Upper Miocene.

*Locality*: Northern flanks of Douglas Mountain on the Weller Ranch, Moffat County, Colorado.

*Principal Characters*: Symphysis of lower jaws relatively long, closely approaching condition shown in "*Trilophodon*" *giganteum*.<sup>38</sup> Lower incisors rounded, slightly converging toward the apices as in "*Trilophodon*" *osborni* and somewhat suggesting the condition found in "*T.*" *giganteum*.<sup>39</sup> Upper tusks relatively long, laterally compressed, slender, with comparatively narrow and light enamel band. Occipital

<sup>34</sup>Dr. O. P. Hay (Pan-American Geologist, Vol. XXXIX, 1923, p. 111) states that *Trilophodon* has no standing as a generic name. He also regards *Tetralophodon* as a synonym of *Gomphotherium* and raises *Anancus* Aymard to full generic rank, though it was sunk as a synonym by Lydekker (Cat. Foss. Mamm. in B.M. IV, 1886, p. 52). Osborn and Frick appear to retain the name *Trilophodon*, the latter using it with *Serridentinus* in parentheses.

<sup>35</sup>*Cf. Evolution, Phylogeny, and Classification of the Mastodontoidea*, Bull. Geol. Soc. Amer., Vol. XXXII, 1921, pp. 327-332.

<sup>36</sup>Dedicated to Mr. Childs Frick in recognition of his great interest in vertebrate paleontology.

<sup>37</sup>Horizon named after Wm. Weller whose ranch is located on the horizon, where the type specimen was found.

<sup>38</sup>Amer. Mus. Novitates, No. 1, Jan. 31, 1921, Fig. 4, c. Outline view of lower jaws of *T. giganteum*.

<sup>39</sup>In using the illustrations in papers cited it is presumed that the specimens are correctly delineated.

plate of skull well rounded from side to side. Second and third molars fully developed.

*Serridentinus fricki* is provisionally placed between *Trilophodon* ("Tetralophodon") *osborni* Barbour<sup>40</sup> and *Trilophodon* (*Serridentinus*) *pojoaquensis* Frick,<sup>41</sup> perhaps closer to "*T.*" *osborni*. The species from Brown's Park is separated from *S. pojoaquensis* Frick by its longer and slenderer tusks, narrower and lighter enamel band, and the more anterior location of the infraorbital foramen. Furthermore, the paratype of Frick's species (Skull No. 21,125 A. M. N. H.) has a shorter and higher cranium, the occipital plate almost square transversely, from side to side with very little forward rounding at the base of the zygomatic arches, while this region in our species is much more rounded.

While there are general similarities between the skull of *S. fricki* and the illustrations of "*T.*" *osborni* Barbour, there are, however, differences in details of considerable importance. In the lower jaw, according to Barbour's illustrations and text, the vertical ramus of the larger individual from Nebraska described by him is relatively longer. The symphysis is actually shorter than in the specimen from western Colorado here described. From Barbour's measurements I also conclude that his species has a relatively thicker jaw.

In comparing the illustrations and measurements of the skull, which Professor Barbour associates with the lower jaws of "*Trilophodon*" *osborni* Barbour, the differences between "*T.*" *osborni* of Barbour and *S. fricki*, appear even greater. The total length of the skull of Barbour's type is actually less than that in our specimen, while the lower jaws are relatively longer and thicker as noted. The tusks of the Nebraskan species are short and heavy as in Frick's species *T. pojoaquensis*. On the other hand the tusks in the specimen from Western Colorado are long and rather slender. The relative measurements of the Coloradan and Nebraskan species are all rather discordant. If the skull and lower jaws of "*Trilophodon*" *osborni* Barbour are correctly associated, they bring to light a remarkable condition. The upper tusks, though well formed and strong, do not reach to the front of the symphysis of the lower jaws and apparently never did reach the anterior part of the incisors to protect them in any way, or assist in their function: in fact the illustration by Professor Barbour indicates the upper tusks to be of seemingly little or no use, as Barbour himself states. This is truly a most curious anomaly not usually encountered in morphological studies.

<sup>40</sup>Amer. Jour. Sci., Vol. XLI, 1916, p. 522, four text-figures. Neb. Geol. Surv., Vol. IV. 1917, p. 499-512, twelve text-figures.

<sup>41</sup>Bull. Amer. Mus. Nat. Hist., Vol. LVI, 1926, p. 142, figs. 1, 22a, 26, 27, and other figures of referred material.



As has been stated, the skull and lower jaws of the specimen from the Brown's Park sediments were found perfectly articulated. In this species it is clear that the upper tusks touched the lower when the jaws were in motion and thus the tusks, upper and lower, functioned in a perfectly normal manner. The apex of the upper tusk is sharpened from inner and outer wear. This wear is towards the enamel band in such a way as to give the latter a lance-shaped outline (See Pl. XII). The enamel band is 50 mm. wide at the alveolar border and decreases almost imperceptibly towards the apex where it is abraded. The first and second upper cheek-teeth are worn, but it is quite clear that they each had three cross-crests.<sup>42</sup> The last upper molar is very little worn and is in fine condition for detailed study, (See Pl. XIV, figs. 6 and 7).

The lower tusks are in general shape and proportion, quite similar to those in "*Trilophodon*" *osborni*, as described and illustrated by Professor Barbour. In the lower jaw there are only two molars on either side, which apparently agree in most details with those of "*T.*" *osborni*. The first cheek-teeth are well worn, but plainly show the three cross-crests. In the present species there are two posterior tubercles, or what may be considered as a heavy cingulum, which do not appear to be present on the corresponding tooth in "*T.*" *osborni* as illustrated by Barbour (*l. c.* p. 505, fig. 7). The last molar has three cross-crests and a large heel. The latter may be regarded as a cross-crest. The posterior cingulum consists of a low mammilated ridge, which rises at the postero-external angle of the crown, forming two accessory cones as shown on Pl. XIV, fig. 8 and 9. In Barbour's illustration of the last lower molar (*l. c.* fig. 7) there is indicated a mammilated cingulum on the antero-external angle, which is not present in our specimen.

## MEASUREMENTS

Skull, greatest length including incisor.....	1555 mm.
Skull, occiput to incisor alveolar border.....	950 mm. <sup>43</sup>
Skull, occiput to infraorbital foramen.....	600 mm.
Skull, occipital condyle to and including first cheek-tooth.....	815 mm.
Skull, occipital condyle to last molar.....	475 mm.
Skull, transverse diameter at posterior portion of zygomatic arch.....	680 mm. <sup>43</sup>
Skull, total length of upper cheek-teeth.....	350 mm.
Skull, antero-posterior diameter of first cheek-tooth.....	84 mm.
Skull, greatest transverse diameter of first cheek-tooth.....	64 mm.
Skull, antero-posterior diameter of second cheek-tooth.....	117 mm.
Skull, greatest transverse diameter of second cheek-tooth.....	75 mm.
Skull, antero-posterior diameter of last cheek-tooth.....	162 mm.

<sup>42</sup>The anterior upper cheek-teeth had fallen out, but were found close to their relative positions. the one in the right jaw fits perfectly in the partly preserved alveolus.

<sup>43</sup>Indicates measurements in part estimated.



Skull, greatest transverse diameter of last cheek-tooth.....	82 mm.
Lower jaw, greatest length including incisor.....	1292 mm.
Lower jaw, from articulating condyle to posterior edge of symphysis.....	734 mm.
Lower jaw, posterior border of symphysis to and including incisors.....	620 mm.
Lower jaw, articulating condyle to and including first cheek-tooth.....	610 mm.
Lower jaw, posterior border of vertical ramus to last molar.....	290 mm.
Lower jaw, vertical diameter of ramus opposite last molar.....	170 mm.
Lower jaw, vertical diameter of ramus at first molar.....	175 mm.
Lower jaw, vertical diameter of symphysis midway between incisors and posterior border.....	125 mm.
Lower jaw, total length of lower cheek-teeth.....	285 mm.
Lower jaw, antero-posterior diameter of first cheek-tooth.....	120 mm.
Lower jaw, greatest transverse diameter of first cheek-tooth.....	70 mm.
Lower jaw, antero-posterior diameter of last molar.....	172 mm.
Lower jaw, greatest transverse diameter of last molar.....	73 mm.

### VERTEBRAL COLUMN

The vertebral column is represented by the axis, the third cervical, and five dorsals from approximately the middle region. In comparing these with the corresponding parts in the American Mastodon in the Carnegie Museum the neural spine of the axis in the new species is relatively heavier; its anterior border extends more forward, showing that it must have partly protruded over the arch of the atlas; the post-zygapophyses slope more strongly upward than in *M. americanus*; the pedicles are heavier; the neural canal perhaps larger; and the centrum slightly longer than in the more recent species. The third cervical vertebra has no neural spine, while in *Mastodon americanus* there is a slight process. The centrum of this vertebra is little if any longer than in *M. americanus*. From the parts present it seems clear that the neck in the present species was relatively longer than in *M. americanus*.

The dorsal vertebræ lack the neural spines, which have been broken off, but their bases indicate the characteristic backward slope of the spines in the Proboscidea. The neural canal is of large size and the general features of the column in this region, as preserved in the type, are not unlike those of "*Eubelodon morrilli*" illustrated by Professor Barbour (Univ. Studies, April 1914, Vol. XIV, plate XI).

### RIBS

The ribs are represented by many fragments, some with the articulating heads and shafts more or less complete. The third rib of the right side is practically complete. This rib is very nearly equal in length to the corresponding rib in *M. americanus*, though slenderer, indicating a thoracic cavity of large size, as in the case in the Nebraskan species.

## MEASUREMENTS

Axis, greatest height approximately.....	257 mm.
Axis, transverse diameter at post-zygapophyses.....	135 mm.
Axis, transverse diameter at anterior cotylæ.....	185 mm.
Axis, antero-posterior diameter of centrum approximately; measurement taken of posterior face.....	150 mm.
Axis, greatest transverse diameter of neural canal.....	67 mm.
Axis, greatest vertical diameter of neural canal.....	72 mm.
Third cervical vertebra, greatest vertical diameter.....	215 mm.
Third cervical vertebra, greatest vertical diameter of centrum; measurement taken of posterior face.....	128 mm.
Third cervical vertebra, transverse diameter at post-zygapophyses.....	164 mm.
Dorsal vertebra, near the lumbar series, vertical diameter of centrum, posterior face.....	100 mm.
Transverse diameter of same.....	110 mm.
Third rib, length measured along the curve.....	865 mm.

## LIMBS

*Scapula.* The coracoid portion of the scapula is not nearly as heavy as in *M. americanus*; the lower part of the spine is near the articulating surface for the humerus as in *M. americanus*.

*Humerus.* The humerus is represented by the median portion of the right shaft and many fragments. The deltoid ridge extends well down and the shaft suddenly flares, indicating similar though shorter proportions than found in *M. americanus*.

*Radius and Ulna.* The epiphyses of the radius and ulna are not completely coossified with the shaft.

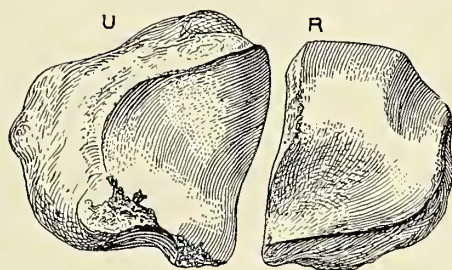


Fig. 21. *Serridentinus fricki* Peterson, sp. nov. Views of distal ends of radius and ulna of the right side. (Type). (C. M. Cat. Vert. Foss., No. 11,379), one-fourth natural size.

*Carpus.* Except the prominent ridge, which separates the facets for the scaphoid and lunar, and the relatively small size of the latter facet, these parts do not show any unusual characters, by which they may be said to differ from corresponding parts in *M. americanus*. The unciform is more deeply excavated on the radial and dorsal faces than in *M. americanus*, and a tubercle of large size rises from the proximal articular surface at the dorso-ulnar angle, which does not appear in the Pleistocene form. The articular surfaces for metacarpals III, IV, and V are dis-



tinctly marked and there is a rugose palmar tuberosity similar to that in *M. americanus*.

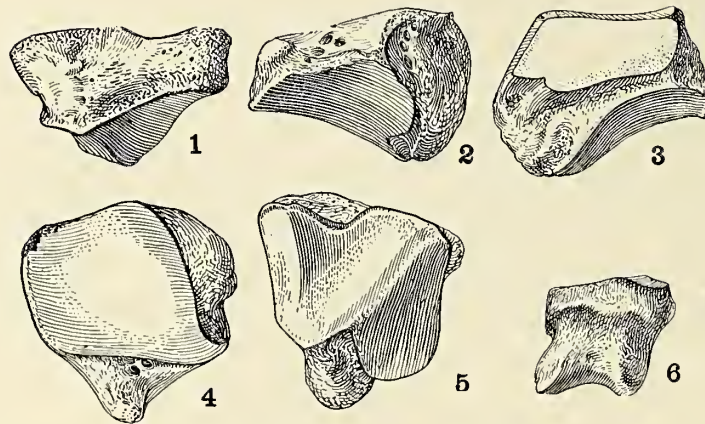


Fig. 22. *Serridentinus fricki* Peterson, sp. nov. 1-5 Ulna of type (C. M. Cat. Vert. Foss., No. 11,379). 1, Oblique dorsal view; 2, Ulnar view; 3, Radial view; 4, Proximal view; 5, Distal view; 6, Dorsal view of phalanx of fifth (?) digit. All figures one-fourth natural size.

*Phalanges.* An asymmetrical phalanx, perhaps of the fifth digit, is all that is preserved of the toes.

Fragments of the femur and both tibiae are preserved.

All the parts found pertain, without doubt, to one individual, as there are no duplicates nor disproportions in the different parts which are preserved.

#### MEASUREMENTS

Scapula, greatest antero-posterior diameter of glenoid cavity.....	174 mm.
Scapula, greatest transverse diameter of glenoid cavity.....	95 mm.
Ulna, greatest transverse diameter.....	112 mm.
Ulna, greatest antero-posterior diameter.....	110 mm.
Ulna, greatest vertical diameter (dorsal face).....	55 mm.
Ulna, greatest vertical diameter (palmar face).....	78 mm.
Phalanx, greatest length.....	55 mm.
Tibia, greatest antero-posterior diameter.....	115 mm.
Tibia, greatest transverse diameter.....	162 mm.

#### A YOUNG SPECIMEN OF *SERRIDENTINUS FRICKI* (?).

##### (Plate XIV)

Approximately three hundred meters from where the type of *Serridentinus fricki* was found and in a slightly higher horizon there was found during the season of 1926 a second specimen, a disarticulated skull of a young individual. The best preserved parts of this specimen are the right and left maxillae with the teeth. The high temporal fossa, the delicate malar portion of the zygomatic arch and the position of the infraorbital foramen are like those in the adult specimen described



above and may well belong to the same species. The superior border of the facial region is sufficiently preserved to give the complete vertical diameter of this region of the skull. Between the narial-premaxillary trough, for the proboscis, and the temporal fossa there is a rather narrow margin, but the actual size of the trough for the proboscis cannot be ascertained, because of the incompleteness of the specimen. In this young specimen no parts of the tusks or incisors are present. The first cheek-tooth has two fangs; its crown being triangular in outline. There are four low tubercles, irregularly placed, the external anterior being the largest, the postero-external next in size, an antero-internal ridge-like cingulum, and an intermediate cingular cusp. The shape and position of this tooth suggests that of the second cheek-tooth in *Trilophodon angustidens*,<sup>44</sup> but in the latter the tubercles are differently arranged. In *T. angustidens* the alveolar border is also longer and there are more cheek-teeth simultaneously erupted than in the American species under study. The second cheek-tooth in the present specimen has three cross-ridges, the anterior much worn, but indicating the usual large internal and small external tubercles. The second cross-ridge is better outlined, but no detailed structure of the two main tubercular bodies is shown. The third cross-ridge has three tubercles; an irregularly shaped and larger internal, an oblong intermediate, and a more nearly conical external; the three more or less closely united to form one body or cross-crest. (See Pl. XIV, fig. 2 and 3). Back of the last complete cross-crest there is a heavy cingulum, or rather a spur-like element, which has its origin at the posterior inner angle of the internal tubercle of the last cross-crest, not unlike what may be observed in the tooth of the maxilla of a young "*M. floridanus*" figured by Lucas,<sup>45</sup> and recently used as the type of a new species by Frick (*l. c.*, p. 169, figs. 20A-C. p. 140). Back of this spur there is a basal cingulum, which continues from the inner angle half-way across the base of the crown. The only wear on the succeeding and recently erupted cheek-tooth is on the anterior intermediate tubercle. The anterior cross-crest consists of two closely connected tubercular bodies, an internal and an external. The second cross-crest is also composed of two main cones with smaller cone-like bodies closely adhering. The individual bodies of the third cross-crest are less distinct from one another, so that the wear of this crest would show less separation of the internal and external bodies. Posterior to the third cross-crest is a double cingulum, the anterior of which may be regarded as an incomplete fourth cross-crest, (See Pl. XIV, figs. 2 and 3).

The most noteworthy feature of this young specimen is the presence of the germ

<sup>44</sup>Paleontographica Vol. XVII, 1867, Pl. III, fig. 1.

<sup>45</sup>Trans. Wag. Inst., Vol. IV, 1896, Pl. IV, fig. 10.

for the fourth? cheek-tooth. This tooth was found after extensive excavation of the maxilla immediately above the milk molar in position as figured, (See Pl. XIV, fig. 1). The calcification is sufficiently advanced to give a general description, but the internal face and a portion of the posterior face are disintegrated and lost. On the antero-external portion of the crown is a prominent cone-shaped tubercle, which is separated from the cross-crest back of it by a deep, narrow, cross-valley. The posterior cross-crest is represented only by the external portion, which is only about half the diameters of that of the anterior tubercle just described. Posteriorly there is a low, but prominent cingulum, (Pl. XIV, figs. 4, 5).

## MEASUREMENTS

Dentition: total length.....	194 mm.
First cheek-tooth: antero-posterior diameter.....	24 mm.
First cheek-tooth: transverse diameter.....	21 mm.
Second cheek-tooth: antero-posterior diameter.....	79 mm.
Second cheek-tooth: transverse diameter at posterior cross-crest.....	49 mm.
Third cheek-tooth: antero-posterior diameter.....	104 mm.
Third cheek-tooth: transverse diameter.....	60 mm.
Fourth cheek-tooth: buried in the maxilla, Antero-posterior diameter of the fragment.....	42 mm.

## A RESTORATION OF SERRIDENTINUS FRICKI

(Plate XV)

The preservation of the different parts of the skeleton which have been described led to an attempt to make a restoration of the form of the animal in life. A sketch was admirably executed by Director A. Avinoff (See Plate XV). The long head and neck, and the short limbs, show us an animal probably capable of reaching the ground with its lower incisor tusks. The creature was relatively heavier in body than the American Mastodon and the elephant of today, and no doubt was surrounded by entirely different conditions from those which prevailed in Pleistocene times and which now prevail.

*Parelephas washingtoni* Osborn.

In the Pleistocene formation on Lay Creek, Moffat County, Colorado, about one half mile from Lay Post Office, Mr. M. A. Langley found a left lower molar of a Proboscidean, which was later presented to the Denver Museum of Natural History by Mr. A. G. Wallihan of Lay, Colorado. Upon comparison this lower molar (No. 472, Denver Museum Catalogue) compares very closely with *Parelephas washingtoni* Osborn. The posterior portion of the tooth is broken, but there are sixteen cross-crests present and there were probably from three to five ad-



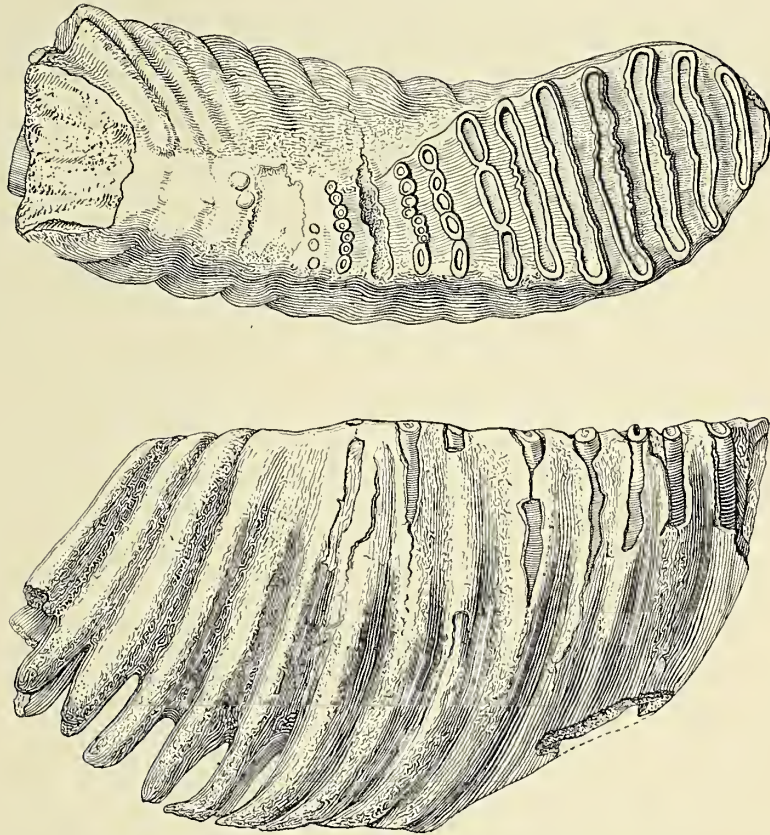


Fig. 23. *Parelephas washingtoni* Osborn. Crown and lateral views of lower left molar, (No. 472, Denver Museum Catalogue). One-fourth natural size.

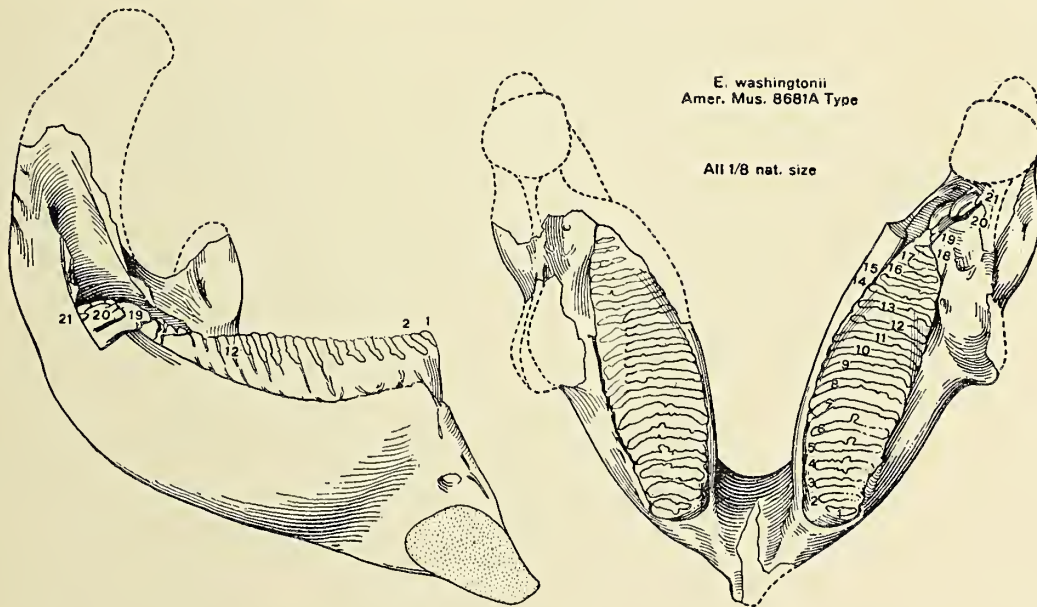


Fig. 24. Crown and lateral views of lower molars of type specimen of *P. washingtoni* loaned by Professor Osborn for comparison with tooth from Pleistocene of Brown's Park, Colorado, shown in fig. 23.



ditional crests in the complete tooth. The size of the tooth, the number of the cross-crests as well as their thickness and degree of crenulation is quite closely identical with the type in the American Museum of Natural History, of which an illustration is herewith published through the courtesy of Professor Henry Fairfield Osborn, President of the American Museum of Natural History, New York.

## SUPPLEMENTARY NOTE.

Professor Henry F. Osborn in a letter to me, dated May 9, 1928, expresses the opinion that the proboscidean, which I have described on p. 111, is *Trilophodon*, and not *Serridentinus*. Osborn regards my proposed species as valid and as being extremely primitive. In a second letter, received June 5, 1928, Osborn suggested that I publish a note changing both the generic and specific names of the specimen in the Carnegie Museum, because it is pre-occupied by Barbour's species *Trilophodon (Amebelodon) fricki*. Osborn repeats his opinion that the specimen in the Carnegie Museum is a good species, representing a very primitive type, between the Middle and Upper Miocene.

Dr. O. P. Hay, writing from the U. S. National Museum, Washington, D. C., under date of May 23, 1928, says that it is his opinion that my *Serridentinus fricki* should be assigned to the genus *Gomphotherium*. For the specimen in the Carnegie Museum Hay proposes the specific name *petersoni*, inasmuch as Professor Barbour of Nebraska has already used the name *fricki* in his description of *Amebelodon fricki*, which Hay puts into the genus *Gomphotherium*.

In a letter dated May the fifteenth 1928, Dr. Julian D. Sears of the United States Geological Survey, states that he is of the opinion that I have misunderstood and therefore misinterpreted (in my notes, pp. 94-96 in the foregoing article) Schultz's reference to the "Bishop conglomerate," in his publication, Bull. 690-C, United States Geological Survey. Not having had an opportunity to visit the regions spoken of in order to verify Schultz, I took it for granted from his remarks on various pages<sup>1</sup>, that, if he had found the soft reddish colored tertiary beds and the "Bishop conglomerate" beds together along the southern flanks of the Uinta mountains, the conglomerate was always found at the base. Since receiving Sears' letter I now add:

From the information we have gained by the discovery of the small and fragmentary fauna (described on previous pages, p. 99, p. 110-111) from the uppermost beds of the sediments in the Uinta basin, I still feel inclined to regard these beds as of Brown's Park age. If the "Bishop conglomerate" beds are found to rest on these Tertiary beds south of the Uinta range, not only have I misunderstood Schultz, but entirely misunderstood the geological age of the so-called "Bishop conglomerate."

<sup>1</sup>Schultz, Bull. U. S. Geol. Surv., 690-C:

p. 56, "The older strata are covered deeply by rocks of Tertiary and later age."

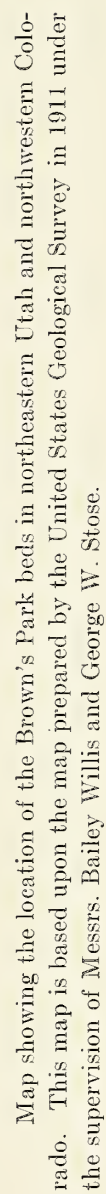
p. 67, "The fault . . . passes beneath the Bishop conglomerate that forms the flat table and of the mountain."

p. 86, "The outcrop of the phosphate bed at the upper margin of the dip slope is also concealed in many places by the Bishop conglomerate . . . A short distance east of the White Rock River, the phosphate beds are concealed by the Bishop conglomerate and Tertiary sediments which cover most of the area on Mosby and Lake Mountains."

p. 87, "In the divide between Dry Fork and Ashley Creek, the outcrop of the phosphate bed is in part concealed by the Bishop conglomerate."







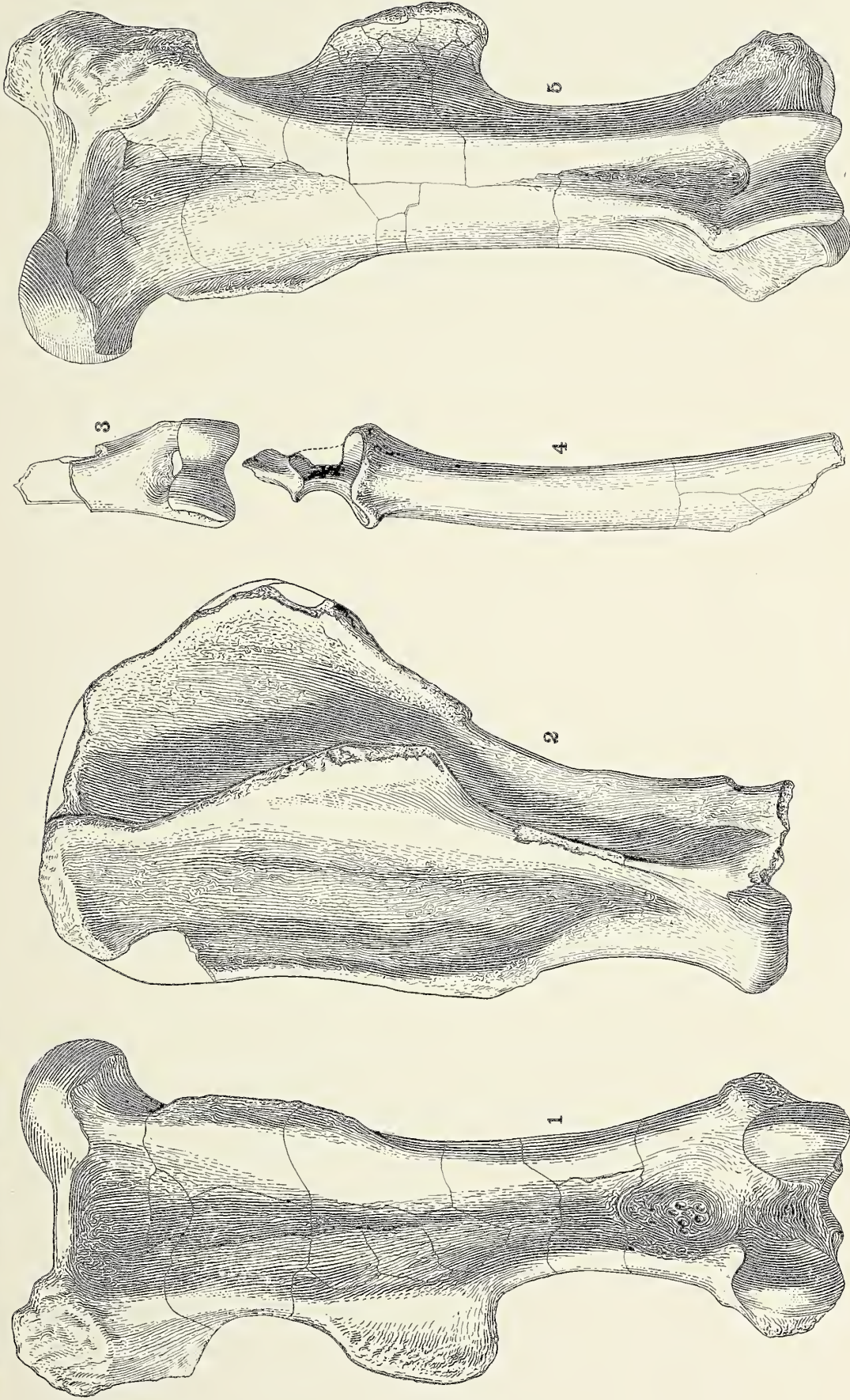






## EXPLANATION OF PLATE X

- Fig. 1. *Aphalops ceratorhinus* Douglass. Posterior view of femur, No. 11,387. One-fourth natural size.
- Fig. 2. *A. ceratorhinus* Douglass. External view of scapula, No. 11,387. One-fourth natural size.
- Fig. 3. Cameloid. gen.? sp.? Anterior view of humerus.
- Fig. 4. Do. Radius and ulna, No. 11,388. One-third natural size.
- Fig. 5. *A. ceratorhinus* Douglass. Anterior view of femur No. 11,387. One-fourth natural size.



For explanation see opposite page.







## EXPLANATION OF PLATE XI

*Serridentinus fricki*, sp. nov. (Type). C. M. Cat. Vert Foss. No. 11,379. All figures one-sixth natural size.

- Fig. 1. External view of rib.
- Fig. 2. Side view of dorsal vertebræ.
- Fig. 3. Anterior view of right tibia.
- Fig. 4. Distal view of right tibia.
- Fig. 5. Side view of axis.
- Fig. 6. Anterior view of humerus.
- Fig. 7. External view of scapula.
- Fig. 8. Anterior view of left tibia.



For explanation see opposite page.



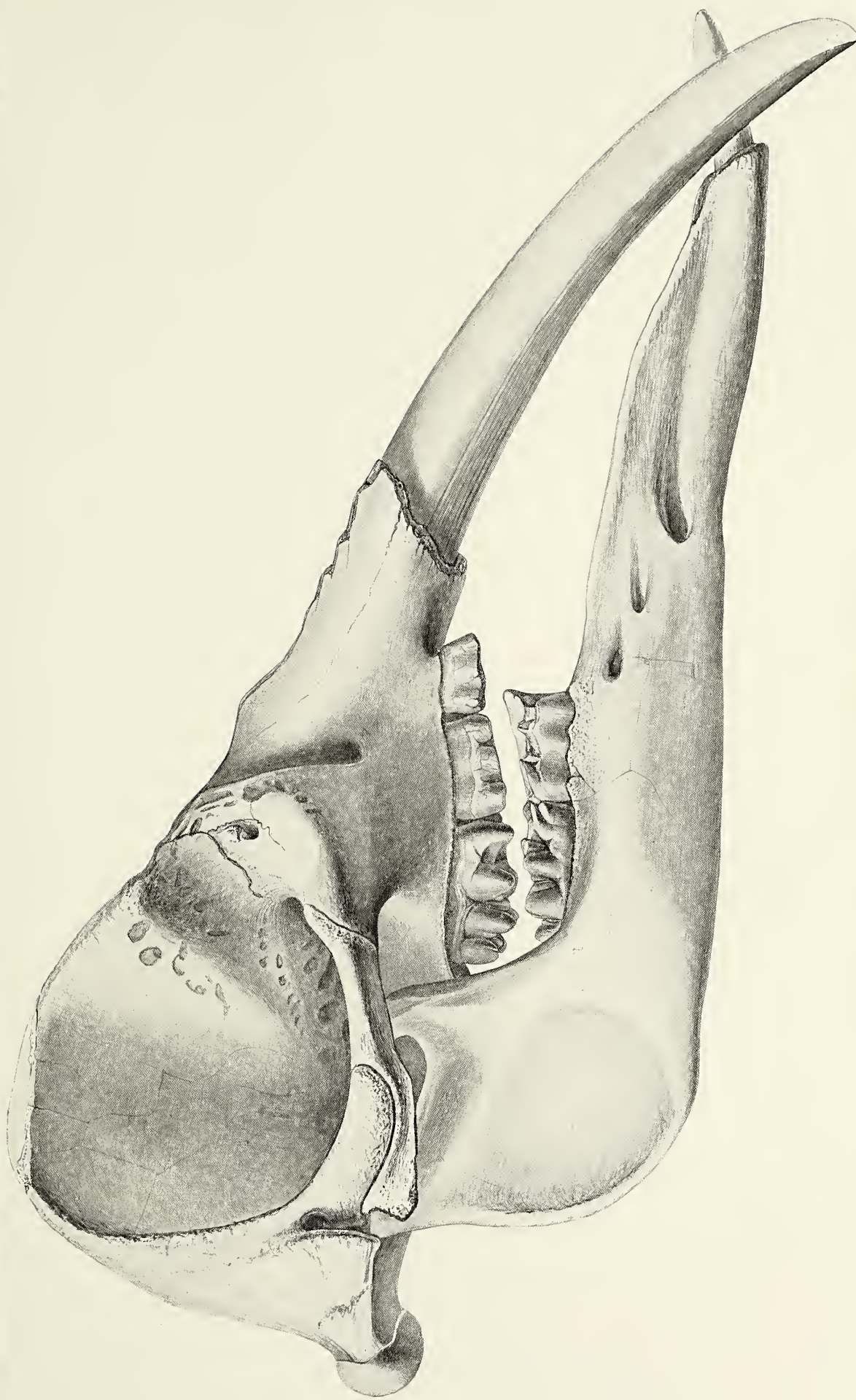




## EXPLANATION OF PLATE XII

Skull and jaws of *Serridentinus fricki*, sp. nov. (Type). C. M. Cat. Vert. Foss. No. 11,379,  
one-sixth natural size.





For explanation see opposite page.

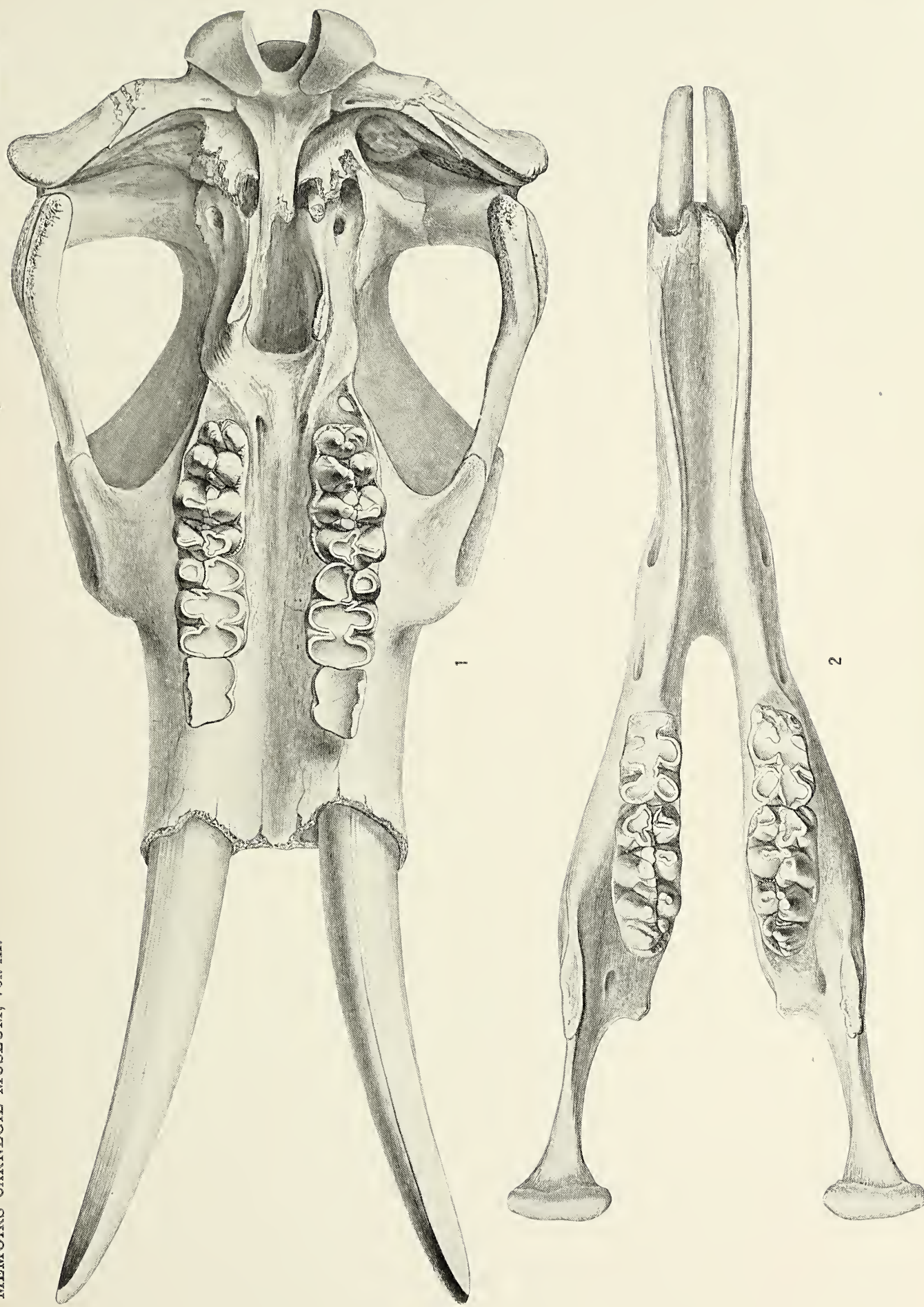






## EXPLANATION OF PLATE XIII

- Fig. 1. Ventral view of cranium of *Serridentinus fricki*. (Type). C. M. Cat. Vert. Foss. No. 11,379, one-sixth natural size.
- Fig. 2. Dorsal view of lower jaw of *Serridentinus fricki*, sp. nov. (Type). C. M. Cat. Vert. Foss. No. 11,379, one-sixth natural size.



For explanation see opposite page.



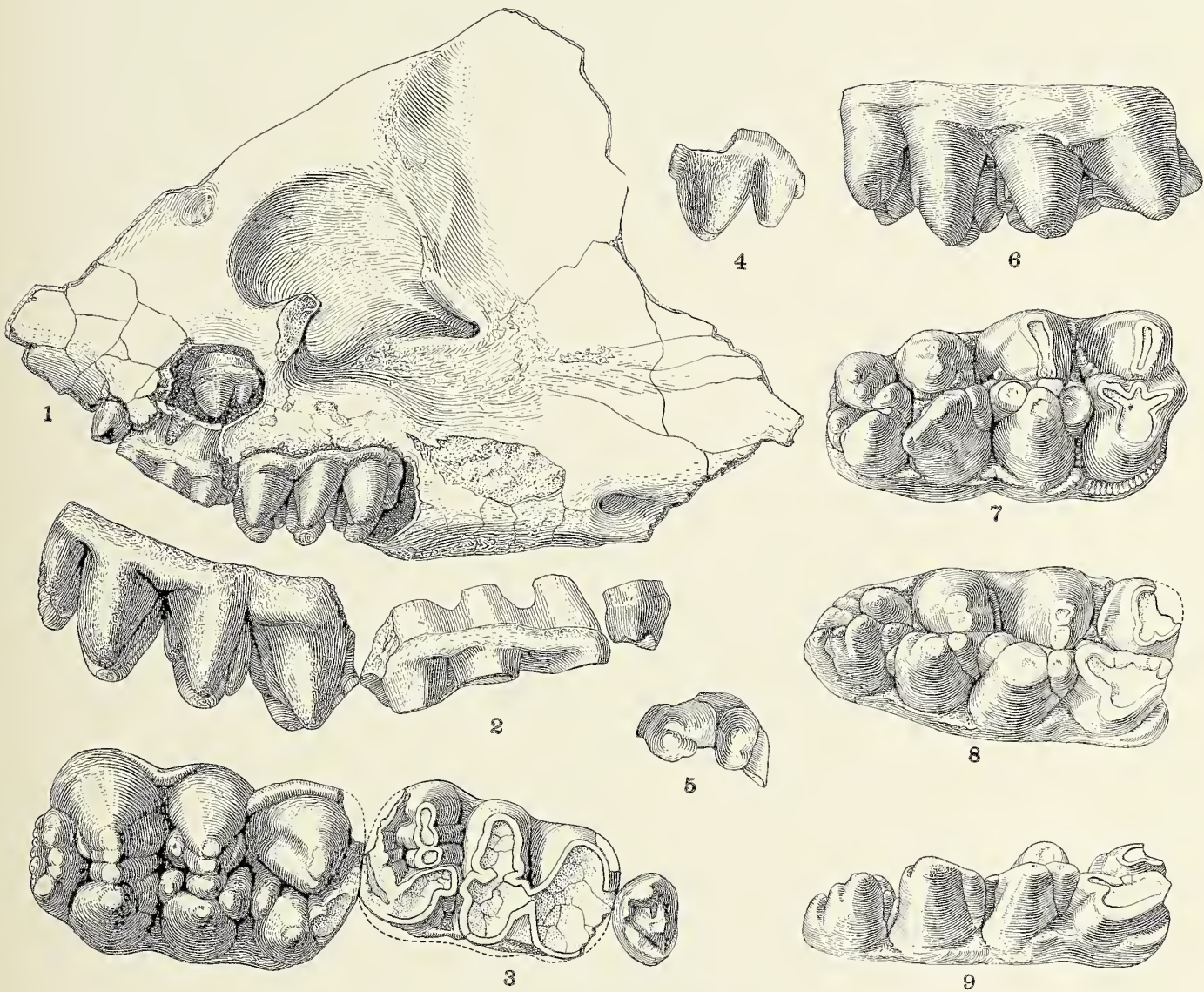




## EXPLANATION OF PLATE XIV

*Serridentinus fricki* Peterson, sp. nov.

- Fig. 1. Left side of facial region of skull of young animal, No. 11,389, one-fourth natural size.
- Fig. 2. External face of cheek-teeth of young skull, No. 11,389, one-half natural size.
- Fig. 3. Crown view of upper teeth of the same specimen shown by figs. 1 and 2, one-half natural size.
- Fig. 4. External view of unerupted cheek-tooth in skull of young animal, No. 11,389.
- Fig. 5. Crown view of the tooth shown in fig. 4.
- Fig. 6. External view of the last upper molar of the type specimen, No. 11,379, one-third natural size.
- Fig. 7. Crown view of the tooth shown in fig. 6, one-third natural size.
- Fig. 8. Crown view of last lower molar, type specimen No. 11,379, one-third natural size.
- Fig. 9. External view of the tooth shown in fig. 8, one-third natural size.

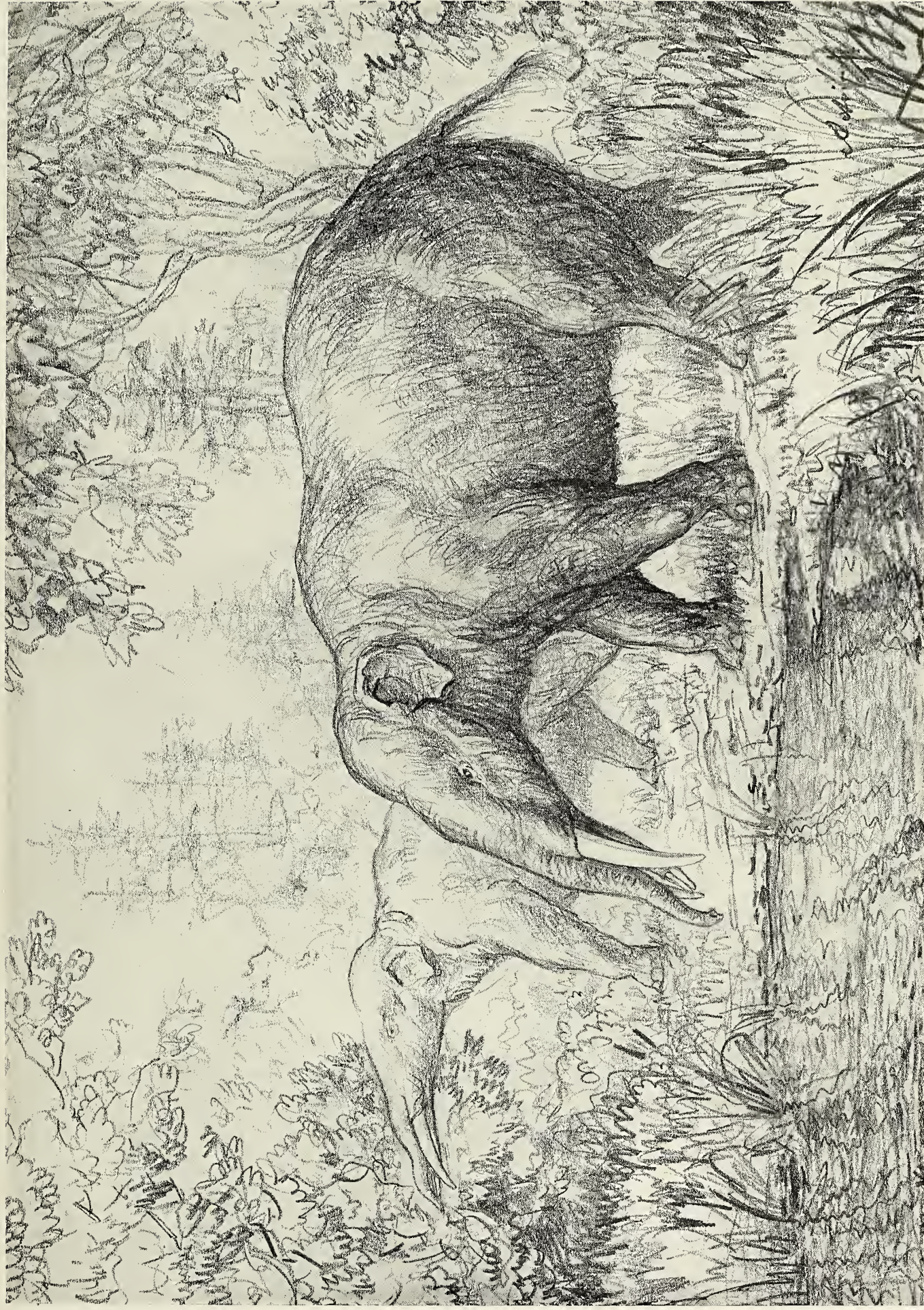


For explanation see opposite page.









Restoration of *Serridentinus fricki* Peterson. Drawn by Andrey Avinoff, Sc.D.



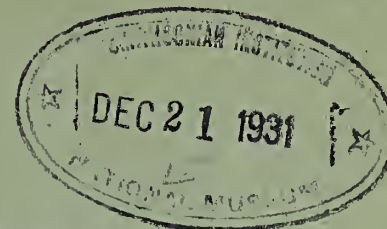




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OSTEOLOGY OF PHENACOCÆLUS TYPUS PETERSON

By O. A. PETERSON

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OSTEOLOGY OF PHENACOCÆLUS TYPUS PETERSON.

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INTRODUCTION.

In 1906-7 the writer briefly described the Oreodont *Phenacocælus* from the material in the Carnegie Museum.<sup>1</sup> Twelve or fourteen individuals of this genus were found in the upper Monroe Creek Beds, near the head of Squaw Creek, Sioux County, Nebraska. The type (No. 1263) consists of the greater portion of a skeleton, found in an articulated position, while the rest of the material is regarded as paratypical, except one specimen, No. 1288. The latter specimen described on page 161, is provisionally regarded as pertaining to a separate species, pending the discovery of cranial and appendicular portions found together.

In the original description it was stated that certain cranial structures of *Phenacocælus* reveal affinities to *Leptauchenia* and *Cyclopidius*. From the material in the Carnegie Museum a comparative study of the cranial structure of *Leptauchenia* and *Phenacocælus* was possible, but the vertebral column and the appendicular skeleton of *Leptauchenia* were lacking. The Museum was fortunate in securing, as a loan, the very complete material of *Leptauchenia* from the authorities of the Princeton University Museum.<sup>2</sup> This material from Princeton has now enabled me to make a more complete comparison between the three genera, viz.: *Phenacocælus*, *Leptauchenia*, and *Merycoidodon*. The main object of the present

<sup>1</sup>Annals Carnegie Museum, Vol. IV, 1907, p. 29-32, Figs. 4, 5.

<sup>2</sup>Since the manuscript of this paper was first prepared, this specimen in the Princeton University Museum has been set up in an articulated position.

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paper, therefore, is (1) to present the osteology of *Phenacocælus* as completely as possible; (2) to compare the latter genus with the much older form *Merycoidodon* from the Oligocene, heretofore supposed to be more or less in the line of ancestry; and (3) to make an especial effort to ascertain the relationship between *Phenacocælus* and *Leptauchenia*. The question of the systematic position of *Phenacocælus* will follow the general osteological description and discussion of comparisons.

The illustrations are reproduced from drawings made by Mr. S. Prentice.

#### Principal Characters of *Phenacocælus typus* Peterson.

*Skull with a general Merycoidodont structure, but proportionally broader and shorter. Orbits directed more upward than in Merycoidodon culbertsoni and more nearly like those in Leptauchenia. Two elongated and narrow foramina on top of the skull, situated at the anterior part of the frontals and near the median line similar to, though smaller than, those of Leptauchenia. Presence of facial vacuities and deep lachrymal pits. Unusually deep pits on posterior face of occipital plate. Short facial region and an elongated cranium. Dentition:  $I_3^3 C_1^1 P_4^4 M_3^3$ ; hypsodont to approximately the same degree as in Leptauchenia; tympanic bulla very large and extending much below the post-glenoid process; sagittal crest low; infraorbital foramen above  $P^3$ ; nasal greatly overhanging anteriorly; limbs and feet short and heavy; metatarsals shorter than the metacarpals. Animal about the size of a domestic sheep.*

#### THE HEAD.

*The Cranium.* (Pl. XVI, fig. 31; Pl. XVII, figs. 11, 12; Pl. XIX.)—The greater part of the right maxillary, and premaxillary bones are preserved in the type, No. 1263. The skull has received considerable lateral crushing, causing an asymmetrical appearance. The occiput is of medium height, with the lambdoidal crests prominent, and a large and deep excavation on either side of the occipital plate just below the junction of the post-temporal ridge with the lambdoidal crest, similar to that found in other genera of this group (*Merychys*, *Mesoreodon*, *Pro-merycochærus*). These excavations occupy a larger portion of the occiput and cause deep lateral emarginations of the supra-occipitals, while in *Leptauchenia* the pits are not present, and the occipital plate is relatively much broader. The median supra-occipital fossa is not deep, and has rough ridges for muscular attachments, which radiate upward and outward from near the median vertical line above the foramen magnum. The condyles are set close to the base, separated inferiorly by a light narrow groove, and with rudimentary accessory facets on the basioccipitals for articulation with the atlas. The foramen magnum is well proportioned in size,

and subovate in outline. The paroccipital process is prominent, as in *Leptauchenia*, trihedral in section, separated from the condyle by a deep fissure, and closely appressed to the posterior border of the tympanic bulla, as in other Oreodonts. The basioccipital is small in transverse diameter, strongly keeled, extending anteriorly between the internal walls of the tympanic bullæ, and joining the basisphenoid uninterruptedly, thus forming an arch gently curved forward to the median pterygoid fossa. The condylar foramen is of large size and is located close to the anterior base of the condyle. The parietal is an elongated, narrow, and wing-shaped bone, the extreme anterior border of which reaches very nearly to the base of the postorbital process of the frontal; the fronto-parietal suture then continues obliquely upward just back of the temporal ridge and unites with its fellow, as in *Merycoidodon culbertsoni*,<sup>3</sup> and most Oreodonts. The sagittal crest, however, is not so prominent as in the Oligocene genus, and the brain-case, as a whole, is fully as large, while the skull represents a smaller animal. The posterior wing of the parietal is not so greatly produced as in *M. culbertsoni*. In this respect it is intermediate between the latter species and *Merychius arenarum*. Along the parieto-squamosal suture there is a very prominent ridge, which separates the temporal fossa into a shallow superior and a deeper inferior portion; there is a large foramen situated in this suture posterior to the middle of its course.

The temporal region is quite like that of *Merychius*. Superiorly, the squamosal extends higher up upon the side of the cranium than in the latter genus, but the shape and position of the zygomatic process, the large external auditory meatus and tympanic bulla, and the closely appressed paroccipital process of the posterior border of the bulla are characters showing great similarity. In *Leptauchenia* and *Cyclopidius* the zygomatic process is more expanded laterally, and does not extend so far forward; the external auditory meatus is relatively larger and is on an even transverse line with the lambdoidal crests and the inion; while the tympanic bulla is fully as large proportionally and the paroccipital process equally appressed to its posterior border as in *P. typus*. The post-glenoid process is heavier than in *Merychius*, but the tympanic bulla extends much below the process, though not nearly as much as in the latter genus. The glenoid cavity is large, it is convex fore-and-aft on the anterior two-thirds; further back it is concave in the same direction; the anterior face of the post-glenoid process has a comparatively less distinct transverse articular surface for the condyle of the lower jaw than is seen in *Merychius* and *Leptauchenia*. The tympanic bulla is, as intimated above, of relatively

<sup>3</sup>A skeleton of this species in the Carnegie Museum, No. 1391, which is very nearly complete, is used for comparison in this work.



enormous size; it is relatively very nearly as great as in *Leptauchenia* and *Cyclopidius*, and in shape it is also somewhat similar to what is seen in those genera.<sup>4</sup> In some of the individuals at hand, the pit for the tympano-hyal is quite large, while that in the type is rather small, and located at the antero-external angle of the base of the paroccipital and the postero-external border of the bulla. The type is much crushed in the region of the basi- and pre-sphenoids; the foramen ovale is, however, observed to be close to the anterior extremity of the tympanic bulla. The pterygoid process of the sphenoid is well developed and extends well down, so as to form a deep median pterygoid fossa. The anterior border of the posterior narial opening is indicated as being well forward in the type. In No. 1276 of the same species the posterior narial opening is complete; its anterior margin is V-shaped, with the apex on an even transverse line with the posterior end of the alveolar border of the maxillaries. Fortunately the right frontal bone is preserved in the anterior median region, so that the external border of the frontal opening is partly preserved. This opening is an extraordinary feature of this genus and most nearly recalls that of *Leptauchenia* and *Cyclopidius*. The vacuity extends farther back than in *Leptauchenia* and is equally as far back as in the latter genus, but does not, however, extend so far anteriorly, and is very much smaller in size. Its function was no doubt the same as that in the genera mentioned. The supra-orbital foramen (in No. 1276) is closer to the posterior border of the frontal vacuity than in *Leptauchenia* and *Cyclopidius*. While the posterior boundary of the frontal is not unlike that in the Oreodonts generally, the anterior region (No. 1276) presents some very peculiar characters, *i. e.*, the narrow and elongated tongue of bone along the median line, which borders the frontal vacuity internally, joins its fellow on the median line, and comes in contact with the nasal anteriorly. The most anterior portion of the frontal is only 21 mm. from the anterior narial opening; from this point the fronto-nasal and fronto-maxillary and lachrymal sutures are only slightly diverging, so as to form a spear-shaped process like that in other Oreodonts. The external border of this process is abruptly convex, due to the large and deep infra-orbital fossa and the facial vacuity. Superiorly the frontals are rather flat, with the temporal ridges less developed than in *Leptauchenia*, and about as prominent as in *Merycoidodon culbertsoni*. The anterior border of the postorbital process has a greater backward tilt than in Oreodonts generally, and more nearly suggests that of *Leptauchenia* and *Cyclopidius*. The process is well developed, and, as in other contemporaneous genera, joins the jugal

<sup>4</sup>In one individual, No. 1278, the tympanic bulla is proportionally small, which indicates either variation, or a specific character.



process from below, completely enclosing the orbit. The superior border of the orbit is rather smooth and the orbital wall of the frontal gives to the eye an upward look as in *Leptauchenia*. The orbit is subcircular in outline.

*The Facial Region.* (Pl. XVI, fig. 31; Pl. XVII, figs. 11, 12.)—The palatine of the type is entirely wanting, but in No. 1276 this region is beautifully preserved. The maxillo-palatine suture is U-shaped, with the rounded apex in front, reaching as far forward as the molar teeth. Thus the maxillary forms a considerable part of the hard palate. The posterior nares, as above stated, are of an open V-shape; the anterior apex is even with the back part of the alveolar border of the maxillary.

Externally the maxillary of the right side of the type is complete from the back to a little in front of the infra-orbital foramen; at this point the bone is broken off, but the most anterior part of the maxilla, including the root of the canine and a fragment of the premaxillary in position, is present, though disconnected. Antero-posteriorly the alveolar border is convex, very similar to that of *Merychius elegans*. The infra-orbital foramen, however, is further forward in the present form than in *M. elegans*, and approaches the condition found in *Leptauchenia*. The external wall of the muzzle is inflated by a heavy and broadly convex ridge, which extends obliquely along the face, thus separating the side of the muzzle into two fossæ; the supra-posterior larger and deeper than the antero-inferior. The ridge for the masseter muscle is not strongly developed. In No. 1276 the palatine portion of the maxillary plate is slightly arched from the alveolar border to the median line, especially anteriorly. The posterior palatine foramen is of moderately large size; it is close to the alveolar border opposite P<sup>4</sup>. The anterior border of the palatine is emarginated for the large round anterior (palatine) foramen.

The premaxillary is relatively less robust than in *M. culbertsoni* and approaches more nearly the condition in *Merychius*. The horizontal bars separating the large anterior palatine foramina are usually broken off; when present, they are very delicate, as in *Leptauchenia*. The ascending process of the premaxillary is stronger, but does not extend so high up upon the anterior nares as in *Leptauchenia* and *Cyclopidius*; thus forming the anterior narial border from below for only two-thirds of the distance to the nasals. In *Merycoidodon* the premaxillary touches the nasals, while in *Merychius leptorhynchus* it furnishes less of the border than in the present genus. The premaxillary is always distinctly separated from the maxillary by a suture and not completely coalesced with it, as in *Merycochærus* and *Promerycochærus*.

The jugal reaches well forward on the side of the face and is relatively heavier

below the orbit than in *M. culbertsoni*, though not so deep as in *Merychys* or *Leptauchenia*. The bone is much expanded transversely;<sup>5</sup> its anterior portion forming a prominent part of the inflated ridge of the muzzle above described. The zygomatic process of the jugal is bifurcated in the usual manner for the reception of the squamosal process; the lower part forming a suture with the inferior border of the squamosal process, and reaching back very nearly to the glenoid cavity; while the upper prong is much shorter. The postorbital process of the jugal is proportionally as well developed as in the *Agriochaeridae* generally.

The lachrymal takes up a considerable portion of the side of the face, but the area is almost entirely occupied by the large and deep lachrymal fossa above described. The superior border is emarginated for the facial vacuity. Inferiorly the jugo-lachrymal suture is quite plain and indicates that the lachrymal furnished a considerable part of the anterior border of the orbit. There is a large lachrymal tubercle, and the lachrymal foramen is below this tubercle and very close to the border, but within the orbit.

Unfortunately the nasals are entirely wanting in the type. While other specimens in our series have this region complete Nos. 1276 and 1277 are the best preserved and present interesting features. From the illustration (Pl. XVII, fig. 11) it is seen that they greatly extend in front, more or less as in *Promerycochaerus carrikeri*; laterally they are imperfectly elliptical, while posteriorly they present two parallel and lance-shaped processes, thus forming a serrated suture with the median processes of the frontal (See Pl. XVII, fig. 11). The nasals are not affected from the frontal vacuities as in *Leptauchenia*, and are on the whole more like those of *Merychys*; the length, however, seems to have been subjected to a much smaller evolutionary reduction than in the Merycoidodonts generally.

*The Mandible.* (Pl. XVI, fig. 31; Pl. XIX.)—The lower jaws of the type are represented by the back part of the ascending ramus and the symphysis. The symphysis is deep and strong. The posterior border of the angle is evenly rounded below the inferior sigmoid notch. The latter is rather shallow. The condyle is very slightly injured internally, but indicates that it did not have a great transverse diameter. On the postero-internal face is a broad and plane facet, which extends well down, and the external angle overhangs the temporal fossa in the usual manner seen in other genera. The latter fossa is large and quite deep, but apparently did not extend much below the horizontal line of the teeth, as is characteristic of *Leptauchenia* and most genera of the *Agriochaeridae*. The coronoid process rises steeply; it is in size of the usual proportions, and terminates in a rounded point,

<sup>5</sup>In the type this region has received much lateral crushing.



which projects slightly backward. The superior sigmoid notch is relatively as deep as in *Merycoidodon culbertsoni*.

The lower jaws of No. 1335 are well preserved. They are as heavy as in *M. culbertsoni*, but much shorter; the horizontal ramus is deep, but in the symphyseal region the two rami are more spout-shaped. There is a large mental foramen below  $P_3$ . Posteriorly below the temporal fossa the ramus is very convex from above downward; the inferior border being quite strongly flexed inwardly as in *Leptauchenia*. The symphysis is strong, as in the type specimen, and the coronoid process rises quite steeply. The temporal fossa is large and the angle rounded. The lower jaws are on the whole perhaps more like those of *Merychys* than *Leptauchenia*.

MEASUREMENTS.	Type No.	
	1263	No. 1276
Greatest length of the skull.....	185*mm.	192 mm.
Length from condyles to incisors.....	170*mm.	175 mm.
Length from posterior border of orbit to the incisors.....	102*mm.	98 mm.
Length from posterior border of orbit to the condyles.....	80 mm.	87 mm.
Length of alveolar border of maxillary.....	95*mm.	92 mm.
Length from posterior end of alveolar border to the condyle <sup>6</sup> .....	75 mm.	81 mm.
Greatest transverse diameter of the skull.....	100*mm.	112*mm.
Transverse diameter of condyle.....	28 mm.	33 mm.
Greatest transverse diameter of brain cavity.....	45 mm.	52 mm.
Transverse diameter of frontals at middle of orbit.....	42*mm.	49 mm.
Greatest transverse diameter of muzzle at anterior nares.....		35 mm.
Transverse diameter of the palate at base of incisors.....		18 mm.
Transverse diameter of palate at $P^1$ .....		23 mm.
Transverse diameter of palate at $M^1$ .....		33 mm.
Transverse diameter of palate at $M^3$ .....		33 mm.
Transverse diameter at base of post glenoid processes.....	70*mm.	81 mm.
Transverse diameter of post glenoid process at base.....	10 mm.	16 mm.
Antero-posterior diameter of post glenoid process at base.....	9 mm.	9 mm.
Antero-posterior diameter of tympanic bulla.....	28 mm.	28 mm.
Transverse diameter of tympanic bulla.....	16 mm.	19 mm.
Antero-posterior diameter of the orbit.....	28*mm.	28*mm.
Vertical diameter of the orbit.....	27*mm.	27 mm.
Vertical diameter of jugal below middle of orbit.....	16 mm.	17 mm.

## MEASUREMENTS OF MANDIBLE OF NO. 1335.

Greatest length of mandible.....	137 mm.
Length of alveolar border of mandible.....	91 mm.
Vertical diameter of angle at condyle.....	72 mm.
Vertical diameter of angle including coronoid process.....	82 mm.
Vertical diameter of angle at $M_3$ .....	35 mm.
Vertical diameter of angle at $P_3$ .....	28 mm.
Transverse diameter at base of $P_1$ , both rami included.....	26 mm.

\*Indicates approximate measurement.

<sup>6</sup>The fore-and-aft crushing of the skull causes the apparent shortness of this region in the type.



*Superior Dentition.* (Pl. XVI, fig. 31; Pl. XVII, fig. 1.)—The incisors of Nos. 1277 and 1335 perhaps resemble those of *Merychys elegans* more closely than *Leptauchenia*. The basal cingula on the posterior face of the crowns are less developed than, for instance, in *M. culbertsoni*. The crowns are rather short and the teeth are set very close together in the alveolar border. The canine has the same characteristic trihedral cross-section, which obtains in the true *Merycoidodonts*; antero-internally are the two grooves separated by the sharp edge, which extends parallel with the long axis of the teeth, antero-externally it is convex fore-and-aft, while posteriorly it is vertical and straight by wear with the anterior face of P<sup>1</sup>. The tooth has a strong fang, which causes a prominent eminence opposite to the root on the lateral wall of the muzzle. The first premolar is separated from the canine by a short diastema; the tooth is placed obliquely in the alveolar border, as in *Merychys* and other genera of the family. The proportional reduction in size of this tooth is greater than in *Merycoidodon*; it is somewhat similar to what occurs in *Ticholeptus*, and not nearly so great as in *Leptauchenia* or *Merychys*. The crown is quite hypsodont and the protocone is shifted further forward on the crown, displaying in these particulars marked difference from the older genus *Merycoidodon*.

The second premolar is present in the type and is of the same relative size as in the Oligocene genus *Merycoidodon*. The characters of the tooth, however, are distinctly marked and are easily distinguished from the latter genus; that is, the external face of the tooth in the present genus has a more even surface, with a much less developed median vertical ridge, and the apex of the protocone is more anterior on the crown, more closely approaching that of *Merychys* and *Leptauchenia*. On the anterior face there is a narrow groove bounded at the bottom by a delicate cingulum; the groove is separated from a larger internal cavity by a sharp, vertical ridge, which extends nearly to the apex of the crown, while in *Merycoidodon* the ridge is confined more closely to the base. In the type the internal face of the crown is much worn, so that these characters of the tooth are less distinct, but No. 1335 shows these features more perfectly. There is a second ridge, sometimes less sharp and less developed (the deuterococone), which separates the antero-internal cavity from a much larger posterior fossa; this ridge in *Merycoidodon* is always the more prominent of the two ridges. The posterior fossa is bounded by a heavy cingulum internally and by a long, sharp crest externally. The tooth is quite obliquely set in the alveolar border. P<sup>3</sup> is much damaged in the type. Externally the crown is convex antero-posteriorly with little or no evidence of a median vertical ridge; the apex of the protocone is placed well forward on the crown, and the tooth in detail appears to be rapidly assuming the characters met with in *Merychys*. P<sup>4</sup> presents

characters altogether similar to those in the latter genus; that is to say, the crown is hypsodont, with a considerable antero-posterior concavity of the external face; the inner crescent is less strongly developed, so that in a less worn tooth it appears more like a very strong cingulum, with a widely gaping interspace between the outer and the inner crescents. The internal cingulum is only very faintly represented. Molars one and two are damaged on their internal faces. The external faces more closely resemble such genera as *Cyclopidius*, *Ticholeptus*, and *Merychys*, the median vertical ridges being directed forward to a greater degree, and the concave portions extending less obliquely inward and downward than in *Merycoidodon*. In No. 1335, which has the teeth best preserved, there is a slight anterior and posterior cingulum on  $M^1$ , while externally it is faintly represented and internally entirely wanting. This is also true of  $M^2$ .  $M^3$  is practically complete. It is relatively much longer and narrower than in *Merycoidodon*, and in this respect holds an intermediate position between that genus and *Merychys*. Characters which closely parallel those in, for instance, *Leptauchenia* and *Merychys* are: the more antero-posteriorly compressed and forwardly extended external ribs or buttresses; the great hypsodonty of the teeth; the vertical position of the external faces of the external crescent; and the deeper and more vertically walled interspaces between the outer and inner crescents.

## MEASUREMENTS SUPERIOR DENTITION.

	Type No.
	1263
Antero-posterior diameter of the superior dentition, approximately. ....	97 mm.
Antero-posterior diameter of premolars two, three and four.....	33 mm.
Antero-posterior diameter of molar series.....	48 mm.
Antero-posterior diameter of $P^2$ .....	12 mm.
Transverse diameter of $P^2$ , approximately.....	6 mm.
Antero-posterior diameter of $M^3$ .....	20 mm.
Transverse diameter of $M^3$ .....	14 mm.

*Inferior Dentition.* (Pl. XVI, fig. 31; Pl. XVII, fig. 2.)—The inferior dentition of the type is represented by the roots of the incisors, canine, and portions of the crowns and the fangs of the first and second premolars.

The incisors are very little, if at all, reduced in size, when compared with those of *Merycoidodon*. The canine is incisiform as in the *Oreodonts* generally.  $P_1$  was of rather small size, which may indicate a sexual character. The tooth is set obliquely in the alveolar border; the anterior edge of the crown is preserved and indicates a lance-shaped structure, which is better shown in more complete specimens.  $P_2$  is even more obliquely set in the jaw than  $P_1$  and has two strong roots; the antero-internal face of the crown is preserved, and shows characters similar to those of the preceding tooth.



In No. 1335 the inferior dentition, excepting the incisors and canine, is complete.  $P_1$  is more robust in this specimen than in the type. The tooth is convex externally, has a stronger vertical ridge on the inner face, sharp anterior and posterior edges, and the apex ascends much higher than the teeth back of it; thus the unworn tooth is much like a lance-shaped canine, much as in the Oligocene genus *Merycoidodon*.  $P_2$  is set very obliquely in the jaw, the external face is less convex than in *Merycoidodon*, and the tooth as a whole is very similar to that of *Ticholeptus zygomaticus*, viz., the crown is hypsodont; the internal face is divided into two simple and imperfect cavities by a heavy median ridge, which extends from the apex downward to the base; the anterior cavity is not bordered internally by a cingulum, while the posterior has a faint cingulum represented.  $P_3$  is larger than  $P_2$ , but is less oblique in the jaw. The external face is very similar to the preceding tooth, but the internal face is more unequally divided by a vertical ridge. As in the tooth preceding it, the anterior cavity has no internal cingulum, but the smaller posterior cavity is well margined. In the bottom of this posterior cavity is a thin, sharp ridge in the fore-and-aft direction, which subdivides the posterior cavity. In  $P_4$  the posterior cavity is completely surrounded, the internal crescent being fully developed, forming a complete connection posteriorly and anteriorly. The premolars are on the whole more hypsodont and narrower than those in *Merycoidodon*.

The molars are not unlike those in *Merycoidodon*, though more hypsodont and narrower. The comparatively long and narrow  $M_3$  of *Merychius* is a well marked feature in the present genus.

## MEASUREMENTS INFERIOR DENTITION.

Paratype  
No. 1335

Antero-posterior diameter of inferior cheek dentition.....	90 mm.
Antero-posterior diameter of premolars.....	38 mm.
Antero-posterior diameter of molars.....	51 mm.
Antero-posterior diameter of $P_1$ at base of crown.....	11 mm.
Transverse diameter of $P_1$ at base of crown.....	5 mm.
Antero-posterior diameter of $P_2$ at base of crown.....	10 mm.
Transverse diameter of $P_2$ at base of crown.....	5 mm.
Antero-posterior diameter of $P_3$ at base of crown.....	12 mm.
Transverse diameter of $P_3$ at base of crown.....	5 mm.
Antero-posterior diameter of $P_4$ at base of crown.....	14 mm.
Transverse diameter of $P_4$ at base of crown.....	9 mm.
Antero-posterior diameter of $M_1$ at base of crown.....	13 mm.
Transverse diameter of $M_1$ at base of crown.....	9 mm.
Antero-posterior diameter of $M_2$ at base of crown.....	22 mm.
Transverse diameter of $M_2$ at base of crown.....	11 mm.
Antero-posterior diameter of $M_3$ at base of crown.....	24 mm.
Transverse diameter of $M_3$ opposite anterior crescent.....	12 mm.



*The Vertebral Column.* (Plates XVI-XIX.)—As previously stated the vertebral column of the type No. 1263 was found in position with all the vertebræ interlocked with one another, from the condyle of the skull to the sacrum; the latter is represented by the pleurapophysis of the first sacral, and there are four anterior caudals represented. In No. 1265 the sacrum is imperfectly preserved, and the tail is represented by seven or eight vertebræ next to the sacrum. With the exception of the sacrum and the caudal region we have thus an exact knowledge of the vertebral formula of this genus which may be stated as follows: seven cervicals, fourteen dorsals, six lumbar, ?five sacral, and eight + ?caudals.

*Atlas.* (Pl. XVI, figs. 1, 8, 9.)—In comparing the atlas with that of the well-known genus *Merycoidodon* it is seen that the expanse of the transverse process in the present genus is proportionally smaller, and also that the arterial foramen near the posterior margin on the ventral face of the base of the transverse process is absent. This foramen is apparently quite normal in both *Merycoidodon* and *Mesoreodon*, here used for comparison.<sup>7</sup> The atlas is incomplete in the skeleton of *Leptauchenia* here used for comparison, but from Dr. Sinclair's paper (Proceedings Amer. Philos. Soc., Vol. XLIX, 1910, fig. 1, pp. 197 and 199) it appears that the atlas differs from that of the present genus by a greater development of the dorsal arch and by the presence of the canal for the vertebral artery which perforates the base of the transverse process.

Professor Scott has stated (The Mammals of the Deep River Beds, p. 133) that the atlas of *Mesoreodon* "is rather more like that of the true ruminants than is that of *Eporeodon*." The present genus has the width of the transverse process even more uniform than in *Mesoreodon* and the posterior termination of the process is more prominent than in the latter genus. The vertical diameter of the atlas is very nearly the same as in *Merycoidodon culbertsoni* (due partly to crushing) while the transverse is much less than in that species. The cotyli for the occipital condyle are well rounded, deep, greatly emarginated above, and less deeply separated at their inferior borders than in *Merycoidodon*. The neural spine is quite rugose and proportionally as prominent as in the latter genus. Again, the vertical diameter of the articulation for the axis is greater, while the transverse is less than that of the older type. The neural canal is well proportioned in size, as are also the canals for the vessels.

*The Axis.* (Pl. XVI, fig. 2.)—The axis is on the whole more nearly like that of *Merychius* than *Merycoidodon*. The neural spine and the body is, however, like

<sup>7</sup>The absence and presence of this arterial foramen is apparently varied in these genera since both Wortman (Bull. Amer. Mus. Nat. Hist. Vol. VII, 1895, p. 149) and Scott (Trans. Amer. Philos. Soc., Vol. XVII, 1893, p. 133) state that it is absent in the material which they studied.

that of the latter genus, but the cephalic articular surface has a greater vertical diameter, the odontoid process is broader, more depressed, and more distinctly spout-shaped, and there is no median rounded ridge on the superior face of the odontoid process and centrum as in *Merycoidodon*. The anterior exit of the vertebrarterial canal has a tendency to become bridged over as in *Merychys* and also in the recent peccary; this feature of the present genus is relatively that which obtains in *Promerycochærus carrikeri*, and apparently shows another mark of progress in modification from earlier types. The posterior perforation is smaller than in *Merycoidodon*. The inferior keel is quite prominent and terminates posteriorly in a rugose tubercle, which extends well back under the centrum of the succeeding vertebra, when in position in the neck. In *Leptauchenia* the body of the axis appears to be broader, the odontoid process less spout-shaped, and the transverse process heavier than in the present genus.

*The Third Cervical Vertebra.* (Pl. XVI, fig. 3.)—The chief characteristic difference of this vertebra from that of *Merycoidodon*, and apparently also of *Merychys*, is its proportionally longer neural arch. The tubercle on the inferior face of the centrum also projects downward to a greater degree and suggests that of *Leptauchenia* and also that of *Agriochærus guyotianus* (Bull. Amer. Mus. Nat. Hist., Vol. II, 1895, p. 150). The neural spine is broken off, but the fracture indicates a rather delicate spinous process, which was apparently less developed than in *Merycoidodon*. The zygapophyses are heavy, the posterior having a greater lateral expansion than the anterior, in order to meet the laterally expanded prezygapophyses of the succeeding vertebra. The transverse process has approximately the same relative strength as in *Merycoidodon culbertsoni* and is lighter than in *Leptauchenia*. The arterial canal is rather small.

*The Fourth Cervical Vertebra.* (Pl. XVI, fig. 4.)—This vertebra differs from the preceding only in minor detail. The transverse process is slightly heavier and the process on the inferior face of the centrum is more prominent than in the third cervical.

*The Fifth Cervical Vertebra.* (Pl. XVI, fig. 5.)—The transverse processes and the tubercle on the inferior face of the centrum of this vertebra are damaged; it can be seen, however, that the inferior keel and tubercle are smaller than in the preceding vertebra, a character also shown in the fifth cervical of *Leptauchenia*. The neural spine is also damaged, but the base indicates that the spine is robust and increases in size as in most genera of the family. The vertebrarterial canal pierces the pedicle at the base and is of rather small size.

*The Sixth Cervical Vertebra.* (Pl. XVI, fig. 6.)—The centrum of this vertebra



is more depressed than in the preceding vertebra; the inferior keel is feebly developed; the neural spine is quite robust, the pedicles are heavy, with a larger vertebrarterial canal than in the preceding vertebra; the pre- and postzygapophyses are heavy, and the inferior lamella of the transverse process droops greatly, and undoubtedly is hatchet-shaped in general outline, as is the case in most genera of the family.

*The Seventh Cervical Vertebra.* (Pl. XVI, fig. 7.)—The seventh cervical has the usual broad and depressed centrum and the high neural spine. The transverse process is quite heavy and outwardly projects horizontally and slightly forward; the pedicle is somewhat more compressed antero-posteriorly at the base, so as to cause a deeper intervertebral notch than in the preceding vertebra. There is no vertebrarterial canal. The cervical region as a whole is proportionally as heavy as in *Merychius*, and similar in details of structure.

*The First Dorsal Vertebra.* (Pl. XVI, fig. 10.)—This vertebra has the usual high and very robust neural spine; the spine is perhaps even higher than in *Merycoidodon*; and it is more attenuated and of greater antero-posterior diameter than in *Leptauchenia*. The centrum is depressed with a heavy and irregularly shaped keel. The anterior surface for the preceding vertebra is strongly convex and the capitular and tubercular facets for the first rib are separated only by a narrow and rather shallow groove on the base of the transverse process. The posterior face of the pedicle and the superior face of the centrum are quite deeply emarginated, forming a deep intervertebral notch, but the notch is not continued so far back on the anterior face of the transverse process as, for instance, in *Merycoidodon culbertsoni*. The postzygapophyses are less distinctly separated than in the latter species, and just above the facets, at the base of the neural spine, is a deep, round pit, which is similar to that in *Merychius*.

*The Second, Third, Fourth, Fifth, Sixth, and Seventh Dorsal Vertebrae.* (Pl. XVI, figs. 11 to 17.)—In receding order the centra of this series become less depressed vertically, more sharply and distinctly keeled, and the transverse processes decrease in length. The neural spines become gradually reduced in size and more backwardly inclined from the first to the last vertebra in this series. In *Leptauchenia* the neural spines have the antero-posterior diameter smaller. The proportionally greater vertical, and smaller transverse diameters of the centra in this series of dorsals, are striking characters, which differ from what is seen in *Merycoidodon*, in which the centra of the corresponding series are broader and vertically more depressed.

*The Eighth, Ninth, Tenth, and Eleventh Dorsal Vertebrae.* (Pl. XVI, figs. 17 to 21).—This second series of dorsals has characters quite distinct from those of



the anterior series. The neural spines in these assume a more vertical position and have a greater antero-posterior diameter at their summits. The centra, however, continue high and narrow, as in *Promerycochærus carrikeri*, and unlike those in *Merycoidodon culbertsoni*, which have the corresponding centra much depressed and expanded transversely, somewhat like those in the recent peccary. The transverse processes are higher up, and the ascending mammillary processes over the prezygapophysis gradually increase in length and prominence from the first to the last vertebra in this series. There are no distinct intervertebral foramina found on the sides of the pedicles.

*The Twelfth Dorsal Vertebra.* (Pl. XVI, fig. 21.)—This bone is chiefly characterized by having less perfectly interlocking prezygapophyses than is the case in *Merycoidodon* and *Promerycochærus*. The postzygapophyses, on the other hand, have the articular surfaces rounded and similar in character to those of the lumbar series. The neural spine of this vertebra is more vertical than in those preceding it. The transverse process is located well forward on the side of the centrum and has an articular surface for the tuberculum of the rib, as in *Promerycochærus carrikeri* and as in the eleventh dorsal in *Merycoidodon culbertsoni*. The centrum is high, narrow, and more gradually tapering downward, and consequently presents a sharper and more prominent keel than in *Merycoidodon*.

*The Thirteenth Dorsal Vertebra.* (Pl. XVI, fig. 22.)—The neural spine of this vertebra has the true anticlinal position, while the spine of the vertebra preceding it is more nearly vertical. The transverse process is also less developed and there is no facet for the tubercle of the rib.

*The Fourteenth Dorsal Vertebra.* (Pl. XVI, fig. 23.)—On the left side of the centrum of this vertebra is preserved a facet, which definitely indicates that the bone supported a small rib. Furthermore, there were found fourteen ribs on each side in very nearly their relative positions and more or less complete, leaving no doubt that we are here dealing with the last thoracic vertebra<sup>8</sup>.

The centrum is high, narrow, and sharply keeled. The transverse process is quite well developed and occupies a median antero-posterior position on the upper part of the side of the centrum. The neural spine is broad antero-posteriorly, much compressed laterally and the pre- and postzygapophyses have a lumbar pattern. The vertebra as a whole is quite suggestive of the corresponding bone in *Leptauchenia*. It is also similar to the corresponding vertebra in *Promerycochærus carrikeri*, but with the keel less produced.

<sup>8</sup>In the skeleton of *Leptauchenia decora* at Princeton (No. 10773) here used for comparison, there are fourteen dorsal vertebræ. From Sinclair's studies (*l.c.* p. 198) this fact is already known.

*The First Lumbar Vertebra* (Pl. XVI, fig. 24.)—The transverse process of this vertebra suddenly increases in size, the antero-posterior diameter being twice that of the bone preceding it; the free end is also broader and more attenuated; there are otherwise only very few differences between the two bones.

*The Second, Third, Fourth, and Fifth Lumbar Vertebrae.* (Pl. XVI, figs. 25 to 28.)—This series of lumbar vertebrae are so similar to one another that a description for each one is not regarded as necessary.

The centra, when compared with those in *Merycoidodon culbertsoni*, are high and narrow, the transverse processes relatively somewhat shorter, and the neural spines less forwardly inclined. In *Phenacocælus typus* the transverse processes in receding order gradually increase in their antero-posterior diameter. The greatest antero-posterior diameter of the centrum appears in the fourth lumbar; the neural spine, which is wanting in the material examined, may also be in this vertebra the largest. Posteriorly, at the base, the neural spine of the fifth lumbar vertebra is less compressed transversely than in the preceding vertebra. In *Leptauchenia* the centra are somewhat more depressed, the transverse processes longer and more compressed fore-and-aft than in *Phenacocælus*, while the neural spines are similar in the two genera.

*The Sixth Lumbar Vertebra.* (Pl. XVI, fig. 28.)—The centrum is more depressed and shorter than in the preceding vertebrae, but in comparison with that of *Merycoidodon* it is high, and is more nearly like the centrum in *Merychius*. The transverse process is shorter and the antero-posterior diameter of the neural spine less than in the vertebrae in advance of it. The left transverse process and post-zygapophysis are wanting, but on the right side the lamina bearing the post-zygapophysis of the first sacral vertebra was found in position in the rock, so that the number of lumbar vertebrae in this specimen is regarded as correct. (See Pl. XVI, fig. 35).

*The Sacrum.* (Pl. XVI, fig. 35.)—Unfortunately in the type the sacrum is represented only by the right pleurapophyses and part of the prezygapophysial process of the first sacral vertebra. From the imperfectly preserved sacrum of No. 1265 it is possible to determine that the ilium is supported almost entirely by the pleurapophyses of the first sacral as in *Merychius*. There were probably five or six sacral vertebrae as in *Leptauchenia*.

*The Caudal Vertebrae.* (Pl. XVI, fig. 30.)—As indicated by the proximal eight caudals of the type, the tail, though of considerable length, was apparently not as long as in *Merycoidodon*. The neural arch soon disappears, the third caudal al-



ready having an imperfect canal, and the zygapophyses and neural spines are of rather small development. The transverse processes of the present series are, however, quite prominent.

## MEASUREMENTS

Length of vertebral column from condyles of skull to sacrum, all curves of the column included.....	605 mm.
Cervical region, length.....	125 mm.
Dorsal region, length.....	305 mm.
Lumbar region, length.....	160 mm.
Atlas; antero-posterior diameter.....	33 mm.
Atlas; transverse diameter.....	56 mm.
Atlas, transverse diameter of condylar articulation.....	31 mm.
Atlas, vertical diameter of condylar articulation.....	17 mm.
Atlas, greatest vertical diameter.....	28 mm.
Axis, greatest vertical diameter.....	44 mm.
Axis, transverse diameter of transverse processes.....	32 mm.
Axis, antero-posterior diameter of centrum, odontoid process included.....	36 mm.
Axis, length of odontoid process.....	11 mm.
Axis, vertical diameter, hypapophysis included.....	15 mm.
Axis, transverse diameter of centrum, posterior measurement.....	14 mm.
Axis, transverse diameter at articulation for atlas.....	30 mm.
Fourth cervical; antero-posterior diameter of centrum.....	21 mm.
Fourth cervical; vertical diameter of centrum, hypapophysis included.....	19 mm.
Fourth cervical; vertical diameter of hypapophysis.....	9 mm.
Fourth cervical; transverse diameter across transverse processes.....	30 mm.
Fourth cervical; transverse diameter of centrum, posteriorly.....	13 mm.
Seventh cervical; antero-posterior diameter of centrum.....	18 mm.
Seventh cervical; transverse diameter of centrum posteriorly.....	18 mm.
Seventh cervical; vertical diameter of centrum, posteriorly.....	11 mm.
First dorsal; antero-posterior diameter of centrum.....	18 mm.
First dorsal; transverse diameter at transverse processes.....	38 mm.
First dorsal; transverse diameter of centrum, posteriorly.....	22 mm.
First dorsal; greatest height in its position in the skeleton, approximately.....	75 mm.
Eighth dorsal; antero-posterior diameter of centrum.....	20 mm.
Eighth dorsal; transverse diameter of centrum posteriorly.....	12 mm.
Eighth dorsal; greatest height in its position in the skeleton.....	52 mm.
Fourteenth dorsal; antero-posterior diameter of centrum.....	23 mm.
Fourteenth dorsal; transverse diameter of centrum, posteriorly.....	12 mm.
Fourteenth dorsal; vertical diameter of centrum posteriorly.....	12 mm.
Fourteenth dorsal; greatest height in its position in the skeleton.....	40 mm.
Third lumbar; antero-posterior diameter of centrum.....	27 mm.
Third lumbar; transverse diameter at transverse processes.....	50 mm.
Third lumbar; transverse diameter of centrum, posteriorly.....	17 mm.
Third lumbar; vertical diameter of centrum, posteriorly.....	13 mm.
Third lumbar; greatest height in its position in the skeleton.....	39 mm.



## THE RIBS.

As stated above, there are twenty-eight ribs (fourteen on either side) represented in the type of this genus. Those in front are quite heavy and flattened; they are more expanded at the costal facet than in *Merycoidodon culbertsoni*. The tubercular and capitular facets are close together and the shaft of the rib has approximately the same curvature as in the latter genus. In the mid-dorsal region the ribs are less flattened, and further back they rapidly decrease in size, the thirteenth and fourteenth lacking the tubercular facets. The sternum is not present in the type and there are no sternebræ represented in the material at hand.

## THE SCAPULA, HUMERUS, RADIUS, ULNA.

*The Scapula.* (Pl. XVI, fig. 32.)—Both scapulæ are present in the type. The feeble development of the metacromion on the spine of the scapula in the present genus is an interesting feature. The area from the angle of the metacromion as far as the middle of the spine is rather broad and rugose, but there is no distinct metacromion process, such as is seen in *Merycoidodon culbertsoni* and in *Pro-merycochærus carrikeri*. This lack of a metacromion reveals a significant approach toward the condition in later selenodont artiodactyls and does not point especially toward an aquatic habit. In the recent peccary the thickened border, representing the metacromion, is nearer the suprascapular border than the glenoid cavity. In the present form the direction of the acromion process (*i. e.*, downward and forward) is quite similar to that in *Merycoidodon*, while further up the spine is less curved and slightly overhangs the postscapular fossa. The latter fossa is deeper and a trifle larger than the one in front of the spine. The glenoid border is very heavy and everted, so as to add to the depth of the postscapular fossa; above it terminates in a small and oblong tuberosity at the posterior angle. The coracoid is quite small and terminates in an obtuse hook-like process at the internal face of the head. There is a decided neck, while the blade again expands above, so that the infra- and post- spinous fossæ are of very nearly equal width at the vertebral border. The antero-posterior diameter of the glenoid cavity is approximately the same, while the transverse diameter is less than in *Merycoidodon culbertsoni*, thus presenting a more oblong articulation in the present genus. The sub-scapular fossa is comparatively small. The scapula of *Leptauchenia* is shorter and broader than in *Phenacocælus*, but otherwise this bone in the two genera is very similar.

*The Humerus.* (Pl. XVI, fig. 33.)—The right humerus is quite completely preserved in the type. In correspondence with the oblong glenoid cavity on the

scapula the articulating surface of the head of the humerus has a somewhat greater antero-posterior than lateral diameter, and it is less convex than in *Merycoidodon*. The greater tuberosity is relatively larger, especially in the antero-posterior direction, but rises less above the articulation of the head, while its extent across the entire anterior face is similar to that in *Merycoidodon*. Part of the lesser tuberosity is damaged, but it can be determined that it is relatively as robust and as large as in *Merycoidodon*. The bicipital groove is of moderate size and is apparently more open above than in *Merycoidodon culbertsoni* and *Promerycochærus carrikeri*. On a direct front view the shaft presents a sigmoid curve, which has, to a small extent, been caused by crushing. The deltoid ridge is quite prominent, more so than in *Merycoidodon*. The shaft, though much shorter, is very nearly as heavy and rounded as in *Merycoidodon culbertsoni*.

The distal trochlea is characterized by the same obliquity as in *Promerycochærus carrikeri*. Unfortunately the inner face of the internal condyle is broken off, but, judging from the very broad inter-condylar ridge, the transverse expanse of the distal end must have been considerable. The external trochlea is relatively somewhat smaller than in *Promerycochærus carrikeri* and much smaller than in *Merycoidodon culbertsoni*. This is a marked advance towards the condition found in the recent Artiodactyla. The small part of the internal epicondyle, which is present, indicates that it had perhaps very nearly the same relative size as in *Merycoidodon*. The anconeal fossa is high and rather narrow, the external border overhanging the fossa more than is seen in the latter genus and in *Promerycochærus*. There is a perforation of the thin wall of this fossa, which may, or may not, be a true supratrochlear foramen. The supinator ridge is only moderately prominent.

In *Leptauchenia* the humerus is of the same proportionate length as in the genus under description, but the bicipital groove is larger, the proximal end of the shaft heavier, the portion above the supinator ridge slenderer, and the trochlea and distal end broader.

*The Radius.* (Pl. XVI, fig 34; Pl. XIX.)—The radius is characteristically merycoidodont; thus the broad head and round shaft are at once recognizable features. The external division of the humeral facet of the radius is much reduced, the ridge separating it from the median region is less prominent, while the median and internal facets are proportionally larger than in *Merycoidodon*. This is quite in keeping with conditions found on the distal trochlea of the humerus. The radius shows no indication of coalescence with the ulna, but the head is articulated more firmly with the anterior face of the ulna than in *Merycoidodon*. The broad transverse surface of the head rapidly decreases downwardly, so that the shaft



very soon becomes quite rounded, even more so than is observed in Oreodonts generally. More distally the shaft again arches more backward and is flatter transversely.

The distal end of the radius is more strongly flexed outward than in *Merycoidodon*, so that the manus, when in position, points outward rather unusually. The transverse and antero-posterior expansion are very nearly as great as in *Merycoidodon culbertsoni*. The anterior face is well marked by the broad groove for the extensor tendon. The distal articular facets are injured, especially the one for the scaphoid; however, enough is preserved to indicate the great obliquity of this facet as in the larger Oreodonts (*Promerycochærus montanus*, *P. carrikeri*, and *Merycochærus*) and also to show that the facet was flexed quite high on the radial posterior angle. The lunar facet is of relatively greater transverse diameter than that in *Merycoidodon*, and it has a higher position on the bone than is seen in the latter genus.

The proximal end of the radius in *Leptauchenia* is more suddenly expanded transversely than in *Phenacocælus*. The shaft has a greater forward bow and the distal end has a proportionally greater antero-posterior and less transverse diameter than in the latter genus. The oblique position of the facets for the carpus in *Leptauchenia* is especially similar to that of *Phenacocælus* described above.

*The Ulna.* (Pl. XVI, fig. 34; Pl. XIX.)—The ulna is not reduced and is even comparatively more robust than in *Merycoidodon culbertsoni*. The upper end of the olecranon process was found incomplete, but what remains indicates that it was as heavy as in the Oreodonts generally. In correspondence with the narrow antconeal fossa of the humerus the upper humeral articulation of the sigmoid cavity is small in transverse diameter, when compared with *Merycoidodon*, while the lower portion of the cavity is actually broader than in the latter genus. The internal angle of the humeral articular surface is well developed and extends nearly even with the internal face of the head of the radius. Externally there is a broad facet for the head of the radius. This facet is bounded externally by a very prominent ridge, which continues downward, as the antero-external border of the shaft, and is much more prominent than in *Merycoidodon*. The shaft of the ulna presents a trihedral section in the upper portion, while lower down it is more nearly flat; it is much arched in order to accommodate itself to the curve of the shaft of the radius. Postero-radially is a prominent ridge, which extends from near the distal end one-third up on the shaft and overlaps the posterior face of the shaft of the radius, as in *Promerycochærus carrikeri*. This feature is far more prominent than in *Merycoidodon*. The cuneiform facet has a relatively greater transverse, but somewhat



less antero-posterior diameter, than in the latter genus. Furthermore, the facet is more convex antero-posteriorly and extends higher up upon the bone in front and behind; the pisiform articulation is consequently quite continuous with that for the cuneiform.

The distinguishing feature of most prominence in the ulna of *Leptauchenia* is the great development of the tubercle for the attachment of the internal humeral part of the triceps muscle. This tubercle, located on the antero-internal angle of the upper end of the olecranon process, is proportionally much more developed than in *Phenacocælus* and greater than in any genus of the family known to the writer, *Agriochærus latifrons* from the Oligocene included. In size the ulna of *Leptauchenia* is fully as large, if not larger, proportionally than in *Phenacocælus*. The distal portion of its shaft does not overlap the posterior face of the shaft of the radius as in *Phenacocælus*, as already described.

#### THE CARPUS.

The carpus is actually higher than in *Merycoidodon* and very nearly as broad; otherwise the structure of this region bears a close similarity to the latter genus, with which it is herewith compared.

*Scaphoid.* (Pl. XVII, figs. 5, 6.)—The scaphoid is higher than in *Merycoidodon*, its transverse diameter smaller dorsally, while on the palmar side it is broader. The articulation for the radius is more convex anteriorly and rises more rapidly on the ulnar side,<sup>9</sup> but the posterior part of the articulation is less strongly concave antero-posteriorly. This is due to the less elevated palmar protuberance in *Phenacocælus*. This palmar protuberance is produced rather more radially in the latter form, so that the palmar face is proportionally and actually broader than in *Merycoidodon*. On the ulnar side the bone in the type is more deeply excavated, and overhangs above more in the ulnar direction, so that the superior ulnar angle of the bone reaches over and forms a contact with a corresponding face on the radial side of the lunar.\* The inferior articulation for the lunar is of greater vertical extent than in *Merycoidodon*, but, as in the latter, it continues quite to the palmar face of the scaphoid. The distal surface is unevenly divided by a well-defined ridge, which extends antero-posteriorly and separates the larger facet for the magnum from the smaller facet for the trapezoid. Both facets are concave antero-posteriorly.

The scaphoid of the specimen of *Leptauchenia* at Princeton (No. 15757) is incomplete. It is possible, however, to ascertain from the fragment that the facet

<sup>9</sup>The elevation on the ulnar angle is variable.

for the radius did not extend downward so much on the dorsal face as in *Phenacocælus*, while in the palmar radial region there is a more rapid elevation of this facet, due to the greater elevation of the palmar protuberance in this region. The facets for the magnum and the trapezoid are more nearly subequal in size and separated by a ridge of greater prominence than in *Phenacocælus*.

*Lunar.* (Pl. XVII, figs. 5, 6.)—The lunar is higher than in *Merycoidodon culbertsoni*. Proximally the facet for the radius is deflected lower down on the anterior face of the bone, so that the articulation is more obliquely convex fore-and-aft than in the latter genus. On the anterior face of the lunar there is a horizontal and rugose ridge at the termination of the deflexed articular facet for the radius, which extends quite across the anterior face of the bone, causing the dorsal surface below this band to be concave vertically. Radially the lunar is much excavated and the facet for the scaphoid is less distinctly separated from that of the magnum than is seen in *Merycoidodon*; it is also quite strongly convex antero-posteriorly, and the beak of the lunar reaches well down, but does not come in contact with the head of the third metacarpal. On the ulnar side the bone is excavated deeply, but the prominent elevated lip, near the proximal face of the lunar in *Merycoidodon*, is much less prominent and less overhanging in *Phenacocælus*; the cuneiform facet is also more restricted to the anterior portion of the bone. Distally the lunar is, as in *Merycoidodon*, almost entirely taken up by the somewhat obliquely placed facet for the unciform. The bone has a much smaller transverse diameter posteriorly than in *Merycoidodon*.

The lunar of *Leptauchenia* is broader and lower than in *Phenacocælus*. The facet for the radius is narrower, less convex antero-posteriorly, and has a more oblique position than in *Phenacocælus*. Distally the beak-like process is shorter and placed further from the radial face of the bone than in the genus under description, but the bone rests almost entirely on the unciform as in the latter genus.

*Cuneiform.* (Pl. XVII, figs. 5, 6.)—The cuneiform is quite characteristic. All its diameters, except the antero-posterior, are greater than in *Merycoidodon*. The articular surface for the ulna is more deeply set, the anterior border of the articulation being higher than in the latter form and more closely approaching the condition found in the recent peccary. The anterior face of the cuneiform is less convex than in *Merycoidodon culbertsoni*; and on the radial face there is a deeper excavation above the lunar facet. The latter facet is more convex and higher near the anterior face, then gradually decreases in height posteriorly, while the facet in *Merycoidodon* is slightly convex antero-posteriorly and is as high behind as in front. On the ulnar side the cuneiform greatly overhangs the unciform, even more



so than in *Merycoidodon*. The posterior face is an unevenly convex and rugose surface. The facet for the pisiform is not so close to the ulnar angle of the bone as in the latter genus. On the distal surface the bone has a large cup-shaped facet for the unciform.

In *Leptauchenia* the cuneiform is relatively broader and shallower than in *Phenacocælus*. The articulation for the ulna is quite similar to that in the latter genus, while that for the pisiform is proportionally larger. The articulation for the unciform is also less cup-shaped than in *Phenacocælus*.

*Pisiform*. (Pl. XVII, fig. 5, 6.)—The pisiform, though similarly constructed, is much more delicate than in *Merycoidodon*. The vertical diameter is somewhat greater, while transversely it is much more attenuated, and its entire length is also less than in that genus.

The pisiform of *Leptauchenia* is proportionally somewhat slenderer than in *Phenacocælus*, but otherwise the bone is similarly constructed in the two genera.

*Unciform*. (Pl. XVII, figs. 5, 6.)—The general outline of the unciform is very similar to that in *Merycoidodon*, but a closer examination reveals a number of characteristic differences. The bone in the present genus has comparatively greater vertical and smaller transverse diameter. The proximal surface of the unciform, which supports the lunar and cuneiform, has an unusually even convexity, showing little or no separation between the two facets. On the postero-radial angle of the lunar articulation is a small round facet, which articulates with a corresponding facet on the end of a projecting arm on the ulnar side of the magnum; this is the only point of contact between the latter bone and the unciform. On the anterior face the unciform is slightly convex in all directions, and near the proximal angle is a narrow groove, which extends across nearly the entire width of the bone. Radially the unciform is partly taken up by the articular surface for Mc. III, which is succeeded by a deep excavation further back. The articular facets for the fourth and fifth metacarpals are divided by a prominent ridge directed antero-posteriorly. The latter facets are concave antero-posteriorly, the two facets together forming a saddle-shaped appearance. The facet for the fourth metacarpal has a proportionally smaller transverse diameter than in *Merycoidodon*.

The unciform of *Leptauchenia* available for comparison is not entirely complete, but it is easily determined that the bone is proportionally broader, lower, and the palmar hook shorter than in *Phenacocælus*.

*Magnum*. (Pl. XVII, figs. 5, 6.)—The magnum is proportionally smaller than in *Merycoidodon culbertsoni*. The chief characteristic difference from that of the latter genus is the greater vertical ulnar face of the bone. The lunar facet in the



present genus is less oblique and does not extend over the top of the posterior convex surface as in *Merycoidodon*, but articulates with the lunar laterally. The facet for the scaphoid is the only articulation, which is entirely proximal in the type specimen, and it is much convex antero-posteriorly, with an oblique downward slope from the ulnar to the radial side. Radially the magnum is deeply emarginated for the contact with the trapezoid. The small anterior face is slightly convex and rugose. Distally the bone has one large saddle-shaped facet for the third metacarpal. The palmar hook is less prominent than in *Merycoidodon*, but in the type there is present the characteristic articulation on the ulnar side for a corresponding facet on the postero-radial side of the palmar process of Mc. III. In other individuals the latter character is less noticeable, or entirely wanting in the present genus.

*Trapezoid.* (Pl. XVII, figs. 5, 6.)—The trapezoid is an irregular nodular bone, which articulates with the magnum, as in *Merycoidodon*; and, as in that genus, the distal end is almost entirely taken up by the articular facet for Mc. II. The small round facet for the trapezium is located well down on the posterior face of the bone. As a whole the trapezoid is approximately of the same relative size as in *Merycoidodon*.

*Trapezium.* (Pl. XVII, figs. 5, 6.)—The trapezium is also of the same relative size as in *Merycoidodon*, but there is no facet for the first digit. On the other hand there appears to be a small rounded facet on the ulnar side, which articulates with the postero-radial face of the head of Mc. II.

The magnum, trapezoid, and trapezium are not present in the material of *Leptauchenia* from Princeton here used for comparison.

#### THE METACARPALS AND PHALANGES.

There is no evidence of a pollex in the manus of *Phenacocælus*. The end of the second metacarpal is wanting, as is also that of the fifth. The chief differences between the metacarpals of the present genus and *Merycoidodon* are: the more robust, though perhaps somewhat shorter, Mc. V; and the general broadness and more flattened condition of the metacarpals in *Phenacocælus*. The length of Mc. III and Mc. IV is approximately the same as in *Merycoidodon*; the distal ends are rounded in a similar manner; and the articular surfaces for the carpals are similar.

There are no phalanges of the manus preserved in the type, but from the paratypes it is observed that these bones are depressed as in *Merycoidodon*, and are also fully as long or even longer than in that genus. The terminal phalanges are somewhat more depressed and broader than in *Merycoidodon*.

The metacarpals and phalanges of *Leptauchenia* are incompletely represented

in the material from Princeton here used. However, it is clear that the shafts of the metacarpals appear to be broad and flat, as in *Phenacocælus*. The phalanges of the proximal and median rows are also depressed and broad as in the latter genus, while the unguals in *Leptauchenia* are poorly represented, the only one present being of a lateral digit, and appears to be pointed, high, and rather narrow. From Dr. Sinclair's study of *Leptauchenia* (l. c. p. 197, fig. 1) it would appear that the metacarpals are shorter than the metatarsals approximately in the same proportion as in *Merycoidodon*.

## MEASUREMENTS OF FORE LIMB.

Type No.  
1263

Scapula, height.....	106 mm.
Scapula, antero-posterior diameter at vertebral border.....	75 mm.
Scapula, antero-posterior diameter of glenoid cavity including coracoid.....	24 mm.
Scapula, transverse diameter of glenoid cavity.....	15 mm.
Scapula, greatest depth of spine.....	19 mm.
Humerus, greatest length.....	137 mm.
Humerus, antero-posterior diameter of head.....	37 mm.
Humerus, transverse diameter of head.....	29 mm.
Humerus, transverse diameter of distal end, approximately.....	27 mm.
Humerus, antero-posterior diameter of distal end.....	21 mm.
Radius, greatest length.....	109 mm.
Radius, transverse diameter of head.....	20 mm.
Radius, antero-posterior diameter of head.....	10 mm.
Radius, antero-posterior diameter of distal end.....	10 mm.
Radius, transverse diameter of distal end.....	19 mm.
Ulna, greatest length, approximately.....	140 mm.
Ulna, transverse diameter of sigmoid cavity, inferior part.....	20 mm.
Ulna, transverse diameter of distal end.....	11 mm.
Ulna, greatest antero-posterior diameter of distal trochlea.....	4 mm.
Carpus, height, at ulnar angle.....	20 mm.
Carpus, breadth, proximal row of bones.....	26 mm.
Pisiform, total length.....	18 mm.
Metacarpal III, length.....	53 mm.
Metacarpal IV, length.....	52 mm.

## THE HIND LIMB.

*Pelvis.* (Pl. XVI, fig. 36.)—The right ilium and the anterior part of the ischium are the only parts of the pelvis preserved in the type specimen. The chief point of difference between *Merycoidodon culbertsoni* and *Phenacocælus* at this point is the much heavier and more rugose acetabular border in the latter. The border above the sacro-iliac contact of the ilium is broken off, but on the whole the vertical diameter of the ilium seems to have been somewhat less than in *Merycoidodon*. The fragment of the ischium indicates similarities to the corresponding part in *Merycoidodon*. The acetabulum is partly destroyed, but it is possible to ascertain



that it is quite deep and that the anterior border is heavy and slightly curved backwards, so as to more completely lock the head of the femur than is the case in *Merycoidodon*, and is in this respect more like what is found in *Merychyrus*. Only a part of the cotyloid notch is preserved, which is in all respects similar to that in *Merycoidodon*. From one of the paratypes (No. 1265), it is possible to determine that the pelvis is broad posteriorly, forming a broad pelvic cavity as in *Merychyrus*. The outline of the obturator foramen in this specimen is also present; it shows that this foramen is of the usual size and proportions, and oblong in shape. The ascending process of the pubis is short, though quite robust, and the horizontal ramus was apparently broad transversely.

In *Leptauchenia* the pelvic girdle is proportionally as heavy or possibly even heavier than in the genus under discussion. The transverse expansion, especially along the ventral borders of the ilia, is greater and the pelvic cavity is also apparently fully as great or greater than in *Phenacocælus*, while the ischium and ilium together form a bar of bone more nearly straight in the fore-and-aft direction than in the latter genus. This is due to the smaller prominence of the spine of the ischium and to the less expanse of the ilium in the dorsal direction in *Leptauchenia*.

*Femur*.—It is unfortunate that the femur of the type is represented only by a short section of the shaft, which gives no character worthy of note, beyond the fact that the circumference is similar to that in specimens provisionally referred to another species of this genus, which will be described later. It may be provisionally said that the femur appears to be relatively longer than in *Merycoidodon* and *Leptauchenia*. There is no patella preserved with the type specimen.

*Tibia*. (Pl. XVII, figs. 37-39).—The extreme proximal end of the tibia is broken off, otherwise the bone is complete. The shin-bone is, however, proportionately stouter than that of *Merycoidodon* and also differs from that of *Merychyrus minimus* from the Upper Harrison beds. The cnemial crest is very prominent and overhangs the fibular side of the shaft to a greater degree than in both *Merycoidodon* and *Merychyrus*, and the anterior face of the shaft, below the crest, continues more prominently to the distal end, so that the shaft has a marked obliquity in the postero-fibular direction not seen in the other genera mentioned. The posterior, the tibial, and the fibular faces of the shaft are not unlike what is seen in *Merycoidodon*. Distally, however, the tibia has a greater transverse diameter. The internal malleolus, though somewhat shorter than in *Merycoidodon*, is fully as robust, and has the usually everted free end for a more completely locked ankle-joint; a common feature seen in this family. The trochlea displays the usual oreodont features, viz, the narrow and low external groove, the broader and



much higher located internal groove. The tibial face of the distal end is slightly damaged.

*Fibula.* (Pl. XVI, figs. 37-39.)—The shaft of the fibula appears proportionally as heavy as that of *Merycoidodon*. The distal end is, as usual, enlarged, quite rugose, and with a deep excavation on the tibial face for contact with a well formed facet for the calcaneum.

In *Leptauchenia* the tibia is much more delicate in its general proportions than in *Phenacocælus*. The bone is also relatively longer than in the latter. The cnemial crest does not extend so low, the median region of the shaft is more nearly cylindrical, and the fibular face of the distal end is less excavated for the reception of the fibula. The latter is proportionally slenderer than in *Phenacocælus*.

#### THE TARSUS, METATARSALS, AND PHALANGES.

One of the most significant characteristics of this genus is its broad and short hind foot. The pes is on the whole shorter than the manus, which is a feature differing not only from the *Agriochæridæ*, but from the *Artiodactyla* generally. In *Leptauchenia* the pes is longer than the manus in the usual proportion seen in the family *Agriochæridæ*.

*Calcaneum.* (Pl. XVII, figs. 9-10.)—The tuber of the calcaneum is short and heavy; the tendinal groove is oblique and rather shallow, while the facet for the astragalus on the lesser process is at a more direct right angle than in *Merycoidodon*, so that, when the bone is in position, it throws the free end of the tuber towards the tibial side and the fibular face downward to a greater degree than is seen in the latter genus. The groove for the interosseous ligament is relatively smaller and the anterior face of the cuboid facet is broader than in *Merycoidodon*.

In *Leptauchenia* the sustentacular facet is of relatively greater vertical diameter in order to conform to the higher astragalus, and the tuber is also more trihedral in cross-section than in *Phenacocælus*. Furthermore, when the bone is in position, it has apparently a more direct fore-and-aft position in *Leptauchenia* than in *Phenacocælus*.

*Astragalus.* (Pl. XVII, figs. 7-8.)—The astragalus is broader and lower than in *Merycoidodon culbertsoni* and more nearly like that of *Merycochærus* from the Upper Harrison Beds. Some features of the astragalus also recall that of *Argiochærus major* (Bull. Am. Mus. Nat. Hist., Vol. VII, p. 168, 1895), viz., the great transverse diameter and short neck. The external condyle of the proximal trochlea differs from that of *Merycoidodon culbertsoni* by being more oblique and higher. The external face also overhangs the calcaneal facet and the median groove is

crowded over more to the internal side, so as to cause an unusually small internal condyle. This condition of the external condyle is apparently due to the outwardly forced upper end of the astragalus. The neck, as above stated, is short, but distinctly separates the proximal and distal trochleæ. The facet for the malleolus of the tibia appears as an irregular and rather deep groove on the tibial face, which is chiefly due to a prominently developed knob near the proximal plantar angle. On the fibular plantar angle there is another large rounded excavation for the articulation with the calcaneum. The navicular portion of the distal trochlea is apparently not so deep as in *Merycoidodon* and more like that of *Merycochærus*, but, as in the latter genera, the navicular facet is much larger than the facet for the cuboid. The sustentacular facet is not so deep as in *Merycoidodon culbertsoni*, otherwise it is similar.

The astragalus of *Leptauchenia* has proportionally a greater vertical and smaller antero-posterior diameter than is the case in *Phenacocælus*. The facet for the cuboid is also more oblique and narrower than in the latter genus, but otherwise the bone is in general similar in the two genera.

*Cuboid.* (Pl. XVII, figs. 9-10.)—The cuboid has a broader anterior face than in *Merycoidodon*, which results in a more triangular articulation for the fourth metatarsal. The astragalar facet is extremely concave antero-posteriorly, and terminates in a high ascending border on the plantar angle. The articular surface for the calcaneum is broader anteriorly than in *Merycoidodon*, but holds practically the same angle of elevation before backward. The antero-posterior diameter of the bone is proportionally somewhat less than in *Merycoidodon*, while the plantar process is more alike in the two genera. The articular facet for the fifth metatarsal is distinctly separated from that for the fourth by a raised ridge, which is more prominent posteriorly and gradually fades away near the anterior margin; this facet is somewhat lateral on the posterior angle.

In *Leptauchenia* the cuboid is proportionally higher and the facet for the astragalus is comparatively even, more concave antero-posteriorly, and deeper than in *Phenacocælus*, but in other details the differences are not great.

*Navicular.* (Pl. XVII, figs. 9-10.)—The navicular is low and broad, the articular facet for the astragalus is subtriangular in outline with the apex backward, concave antero-posteriorly, and convex laterally, especially on the fibular side. On the distal face is an oblong flat articulation for the coössified ecto- and meso-cuneiforms. The tubercle on the tibial face is of the same proportion as in *Merycoidodon*, but the plantar hook-like process is flatter and is less produced downward than in the latter.



The palmar process of the navicular in *Leptauchenia* is relatively longer than in *Phenacocælus*, otherwise the bones of the two genera are not unlike.

*Ecto- and meso-cuneiform.* (Pl. XVII, figs. 9-10.)—The coössified ecto- and meso-cuneiform is not so triangular in outline as in *Merycoidodon*, which is due to the much smaller development of the plantar tubercle near the proximal face of the bone in the present species. In all other respects the compound bone is similar in the two genera. In *Leptauchenia* the ecto- meso-cuneiform is oblong, as in *Phenacocælus*.

*Ento-cuneiform.* The ento-cuneiform has a more triangular outline on cross-section than in *Merycoidodon culbertsoni*. The basin-shaped facet for the navicular, the facets on the external face for the compound cuneiforms and Mt. V on the nodular-shaped bone, are all closely similar to those in *Merycoidodon*. In *Leptauchenia* the ento-cuneiform is less triangular on cross-section than in *Phenacocælus*.

*Metatarsals.* (Pl. XVII, figs. 9-10.)—The metatarsals are unusually short and heavy; they are shorter and heavier than the metacarpals, which is a condition contrary to that usually found in the family, except in the genus *Agriochærus*. The second metatarsal is the shortest. The metatarsals increase in length in the following order: the fifth, third, and the fourth. *Agriochærus latifrons* is set up in an articulated position in the American Museum of Natural History and from the figure of the restoration (Bull. A. M. N. H., VII, 1895, Pl. 1) it seems to appear that the metatarsals are shorter than the metacarpals.<sup>10</sup>

The second metatarsal is considerably reduced in length, but otherwise this element is fully as robust as in *Merycoidodon*. The head rises slightly above the head of Mt. III, and there is a small facet for the meso-cuneiform on the proximal face. On the tibial face the bone articulates with Mt. III in the usual manner, and there is a rough surface on the antero-tibial angle of the head, behind which is located the rather large-sized articular facet for the ento-cuneiform. The shaft is more rounded than in any other metatarsal of the pes, but rapidly expands distally, especially on its tibial face, where a heavy and rugose ridge takes its origin near the distal articulation and continues well up upon the shaft. (See Pl. XVII, figs. 9-10). The carina is quite strongly developed, but, as in *Merycoidodon*, entirely confined to the plantar face of the articulation.

The second metatarsal of *Leptauchenia* is lighter and longer in proportion, and the distal tibial face has not the heavy and rugose ridge seen in *Phenacocælus*.

<sup>10</sup>Wortman states (*l.c.* p. 164) that the manus and pes are subequal in length.



The third metatarsal is reduced in length in the same proportion as in *Merycoidodon*. Superiorly the bone is well interlocked by metatarsals II and IV and by the ecto-meso-cuneiforms. The shaft is rather flattened and more strongly arched than in *Merycoidodon*, but distally the articular facet for the proximal phalanx has a less antero-posterior diameter than in the latter genus. The carina is fully as well developed, while dorsally the articular surface extends higher up than in *Merycoidodon*.

Mt. III in *Leptauchenia* is quite similar to that of *Phenacocælus*, except in its greater proportionate length and in the dorsal portion of the articulating trochlea for the first phalanx, which does not extend as high as in *Phenacocælus*.

Metatarsal IV is the heaviest in the series. On the proximal end the anterior portion of the articulation for the cuboid is gently convex from side to side, while on the posterior part of the head there is a strong plantar tubercle, which shares the support for the cuboid to a somewhat greater extent than is seen in *Merycoidodon*; this portion of the facet is more oblique and located higher than the portion in front. On the tibial face is a strong articular lip, which is well fitted into a corresponding pit on the fibular side of Mt. III, and an elongated facet posterior to this lip completes the interlocking condition of the articulation. On the fibular side the articulation for Mt. V is less complicated. The shaft is heavy and slightly more expanded distally than in *Merycoidodon*. When in position in the pes the fourth metatarsal is seen to extend below the third in approximately the same proportion as in *Merycoidodon*.

In *Leptauchenia* Mt. IV is proportionally longer than in *Phenacocælus*, but otherwise there are no noteworthy differences in this bone in the two genera.

Metatarsal V is fully as strongly developed as in *Merycoidodon*. The proximal end is well fitted against Mt. IV on the tibial face, while above there is a small oblong facet for the cuboid. Distally there is a well formed articular facet for the proximal phalanx.

*Phalanges.* (Pl. XVII, figs. 9-10.)—The phalanges of the second digit are all present; those of the other digits are less completely preserved in the type. The phalanges, especially the outer series, are somewhat more depressed and more expanded laterally, than in *Merycoidodon*.

In *Leptauchenia* there is possibly less difference between the length of the fifth and the second metatarsals than is the case in *Phenacocælus*. As before stated, the phalanges of *Leptauchenia* are very poorly represented, but they were possibly somewhat higher and narrower than in *Phenacocælus*.

MEASUREMENTS		Type No.
		1263
Ilium, from anterior border of acetabulum to point of ilium.....	90 mm.	
Ischium, vertical diameter at posterior part of acetabulum.....	29 mm.	
Tibia, length approximately.....	112 mm.	
Tibia, length of fragment preserved.....	105 mm.	
Tibia, antero-posterior diameter of shaft at cnemial crest.....	29 mm.	
Tibia, transverse diameter of shaft at cnemial crest, posterior measurement.....	14 mm.	
Tibia, transverse diameter of distal trochlea.....	23 mm.	
Tibia, antero-posterior diameter of distal trochlea.....	13 mm.	
Calcaneum, greatest length.....	45 mm.	
Calcaneum, antero-posterior diameter of cuboid facet.....	13 mm.	
Calcaneum, transverse diameter of cuboid facet, anterior measurement.....	7 mm.	
Astragalus, greatest height, approximately.....	24 mm.	
Astragalus, greatest breadth.....	19 mm.	
Cuboid, height, anterior measurement.....	10 mm.	
Tarsus, transverse diameter.....	25 mm.	
Metatarsal II, length.....	33 mm.	
Metatarsal III, length.....	46 mm.	
Metatarsal IV, length.....	48 mm.	
Metatarsal V, length.....	37 mm.	
Phalanges 2nd digit, length.....	37 mm.	
Phalanges 3rd digit, length.....	45 mm.	
Phalanx, terminal, 4th digit, length.....	15 mm.	

#### NOTES ON COMPARISON OF PARATYPES WITH THE TYPE SPECIMEN OF PHENACOCÆLUS TYPUS PETERSON.

In the material discussed in the foregoing pages there are some marked variations worthy of brief notice. These variations might (possibly justly) by some students be regarded as of specific value, but, with one exception (No. 1288), hereafter described, I prefer to regard the differences as being individual and sexual.

On comparison of skull No. 1278 with all the rest of the material representing the head in the series before me I detect the following anatomical points, showing<sup>11</sup> that this specimen discloses: (1) a smaller tympanic bulla; (2) a smaller antero-posterior diameter of the postglenoid process; (3) a larger external auditory meatus, possibly located somewhat further back, and more like what is seen in *Leptauchenia*; (4) a general reduction in the relative length of the skull. With the exception of the first and third features noted, I think it is possible, in fact most probable, that the curious appearance of this specimen is due entirely to crushing. At all events I refrain from here establishing a species because of the excessive crushing of the skull. (See Pl. XVIII, figs. 12-13).

Specimen No. 1288 consists of the lower jaws, fragments of the atlas and other

<sup>11</sup>The skull in question is very much crushed antero-posteriorly.



cervicals, two anterior dorsals, a fragment of the sacrum, fragments of ribs, portions of both radii, and the manus fairly well preserved, the right side of the pelvis nearly complete, and a fragment of the left ilium, the right femur very nearly complete, and the head of the left, both tibiæ nearly complete, and the pes well represented. The material indicates an animal of slightly larger size than the type of *P. typus*.

After lengthy and minute comparison of this material (No. 1288 Carn. Mus. Cat. Vert. Foss.) I am finally constrained to designate it as the type of a new species of *Phenacocælus*. The description herewith follows:

***Phenacocælus munroënsis*** <sup>12</sup> sp. nov.

(Pl. XVIII, figs. 1-9)

The cheek-teeth of the lower jaw are somewhat more delicate than in the paratypes, Nos. 1278 and 1335 of *P. typus*, but this may well be a sexual difference, as the dentition is otherwise quite similar. The symphysial region of the lower jaws is less spout-shaped than in the paratypes referred to above, which may partly be due to crushing. The angle is, however, less flexed inwardly, and thus not quite like the condition found in *Leptauchenia*.

The fragments representing the vertebral column of the present specimen do not present any important differences from those in the type of *P. typus*, or in the material of other individuals. In the fore limb, on the other hand, there appear some very marked differences. It is possible to determine from the remains of the radii before me that No. 1288 has a longer and relatively slenderer shaft. Unfortunately the proximal end of both radii are not present, but what remains of the distal end of the shaft, especially of the left radius, it is seen to be very nearly as long as the entire bone in the type. The broken end of the shaft does not display the characteristic broadening immediately below the head, observed in a complete radius of *P. typus*. I feel certain, therefore, that the bone when complete must have been at least 30 mm. longer, which would give a length 15 to 20 mm. over that in the type of *P. typus*. As in the latter, the shaft of the radius is rod-like throughout, a feature more primitive than in *Merycoidodon*. With the exception of the slightly larger size of the specimen under description, there are no characters of importance by which the fore limb differs from the type or paratypes of *P. typus*.

In correspondence with the fore limb the hind limb is also found to be longer

<sup>12</sup>The specific name is based upon the geological locality, the Monroe Creek Beds, at the head of Warbonnet Creek, Sioux County, Nebraska, where the specimen was found.



and somewhat slenderer than in *P. typus*. No differences worthy of note are observed in the pelvis. The femur is long and slender, its head being placed rather more proximally, which to some extent is possibly due to crushing. There is an unusually deep trochanteric fossa and the lesser trochanter is also quite prominent. The shaft, as stated is slender, while the distal end is suddenly expanded both laterally and antero-posteriorly. There is no femur present with the type of *P. typus*. In the tibia, however, one is able to again observe a greater length, otherwise with little or no greater size of the bone. Again, while the tarsals are in general quite similar, the metatarsals are a trifle longer in No. 1288. In this specimen the metatarsals are seen to be very nearly as long as the metacarpals, while those of the type of *P. typus* as noted in the foregoing work, are considerably shorter than the metacarpals.

MEASUREMENTS	Type No.
	1288
Mandible, length.....	150 mm.
Mandible, height at angle, including coronoid process.....	95 mm.
Mandible, depth at M <sup>3</sup> .....	45 mm.
Mandible, depth at P <sup>3</sup> .....	23 mm.
Mandible, length of dentition.....	103 mm.
Mandible, length of molar series.....	50 mm.
Mandible, length of premolar series.....	40 mm.
Radius, length of fragment.....	100 mm.
Carpus, height.....	21 mm.
Metacarpal III, length.....	60 mm.
Metacarpal IV, length.....	58 mm.
Femur, length.....	160 mm.
Tibia, length.....	133 mm.
Tarsus, height at external angle to inferior face of euboid.....	34 mm.
Metatarsal II, length.....	36 mm.
Metatarsal III, length.....	53 mm.
Metatarsal IV, length.....	56 mm.
Metatarsal V, length.....	42 mm.
Phalanges, 2nd digit, length.....	45*mm.
Phalanges, 3rd digit, length.....	48 mm.

#### SUMMARY OF THE MORE IMPORTANT POINTS OF COMPARISON BETWEEN PHENACOCÆLUS, MERYCOIDODON, EPOREODON, AND LEPTAUCHENIA.

The foregoing comparative description of *Phenacocælus* with *Leptauchenia* and *Merycoidodon* was undertaken with the purpose of ascertaining the relationship between these three genera, especially between *Phenacocælus* and *Leptauchenia*.

\*The phalanges were not found in position and their association with the pes should not be regarded as entirely positive.

For greater convenience a summary of the more important points of differences and the osteological similarities between *Phenacocælus* and other genera may be expressed as follows:

*Phenacocælus* resembles *Merycoidodon* more or less closely, throughout the entire skeletal structure. The two genera are alike, (1) in having the dentition numerically as well as in general form, quite similar; (2) in having a short facial region and an elongated cranium (cranium especially long in *Phenacocælus*); (3) by having deep lachrymal pits; (4) by having overhanging nasals; (5) by the location of the infraorbital foramen above P<sup>3</sup>; (6) by having the temporal ridges of similar shape and quite alike in the degree of development; (7) by a general similarity of the detailed structure of the vertebral column; (8) by a similarly large thoracic cavity; (9) by a similarity in most parts of the structure of the limbs; (10) by a general similarity of the manus (except the absence of the pollex in *Phenacocælus*).

*Phenacocælus* differs from *Merycoidodon culbertsoni*: (1) in having the skull proportionally broader and shorter; (2) in having the orbits directed more upward; (3) by the presence of fronto-nasal vacuities; (4) by the enlargement of the lachrymal pits and the indication of facial vacuities; (5) by having deep pits on posterior face of the occipital plate; (6) by the hypsodont cheek-dentition; (7) by having the tympanic bulla of very large size and extending much below the glenoid process; (8) by the feebly developed and low sagittal crest; (9) by the less transverse expanse of the transverse process of the atlas; (10) by the greater vertical and smaller transverse diameters of the neural spines of the anterior dorsals; (11) by having one more dorsal vertebra, and one less lumbar vertebra; (12) by having the carpus proportionally and actually higher; (13) by having the tibia shorter, heavier, and the shaft of somewhat different shape; (14) by having the pes relatively shorter and broader.

In consulting the literature I find the most complete description of *Eporeodon* from the upper Oligocene in the Proceedings of the American Philosophical Society Vol. XXI, 1884, pp. 514-517. In checking up the material of *Phenacocælus* in the Carnegie Museum with the above mentioned description by Professor E. D. Cope I find a number of anatomical similarities in *Eporeodon* and *Phenacocælus*, which are quite naturally to be expected in forms of the same family. The minor differences in the two genera in question are perhaps of an equal number to the similarities. Of the major differences the following may be mentioned: Cope describes a well defined pre-orbital fossa and frontal foramina as present in *Eporeodon tri-*



*gonocephalus*, but he speaks of no indication of facial or fronto-nasal vacuities, which are very characteristic of *Phenacocælus*.

In *Eporeodon socialis* Marsh, (See Fifth Annual Report U. S. Geol. Surv., 1885, p. 299, figs. 128-129) we learn that the length of the fore foot is approximately the same as in *Phenacocælus*, while the hind foot in *E. socialis* is 22 mm. longer. Mc. III in the latter species is 5 mm. longer, Mt. IV, 8 mm. longer, while the height of the carpus is actually less in *Eporeodon* than in *Phenacocælus*. When checked up with the foot-structure of *Merycoidodon culbertsoni* it is found that all the above measurements of *Eporeodon socialis* correspond much better with those in *Merycoidodon culbertsoni*. The remains of both *Eporeodon socialis* and *E. trigonocephalus* are of larger animals than *Phenacocælus*. From the information derived from the literature it may be inferred, that *Eporeodon*, as known, had not specialized in the direction of *Phenacocælus* to a sufficient degree anatomically, to lead us to consider that genus as directly in the phylogenetic line of *Phenacocælus*<sup>13</sup>.

*Phenacocælus* resembles *Leptauchenia*: (1) in the broadening and shortening of the skull; (2) in the tendency of the orbit, to be upward directed; (3) in the presence of fronto-nasal foramina or openings; (4) in having reduced premaxillaries; (5) in the shortening of the facial region; (6) in the enlargement of the lachrymal pits and the presence of facial vacuities; (7) in the hypsodont cheek-dentition and other similarities in the construction of these teeth; (8) in having the tympanic bulla of very large size and extending much below the postglenoid process; (9) in having the infraorbital foramen above P<sup>3</sup>; (10) in having the same number of dorsal and lumbar vertebræ; (11) in having a large thoracic cavity; (12) by having a similar broad and deep pelvic cavity; (13) by the general similarity of the greater parts of the structure of the limbs and feet.

*Phenacocælus* differs from *Leptauchenia* (1) in having larger and more numerous incisors, with the upper canine less rounded in cross-section; (2) in a more feebly developed sagittal crest, and a longer skull; (3) by having more overhanging nasals; (4) by having large and deep lateral excavations on the occipital plate; (5) by a narrower and more backward projecting occiput, together with less developed temporal crests; (6) by a relatively smaller external ear placed lower down; (7) by a smaller development of the dorsal arch of the atlas, and the absence

<sup>13</sup>The restoration of *Eporeodon socialis* recently published by Thorpe (Amer. Jour. Sci., Vol. II, 1921, p. 309) seems to show that *E. socialis* was similar to *Merycoidodon culbertsoni*. Loomis regards the skeletons of *Merycoidodon* and *Eporeodon* as closely similar (See Bull. Amer. Mus. Nat. Hist., Vol. LI, 1924, p. 9). Finally, if Thorpe's contention proves true that the sediments on the North Fork of the John Day are of later origin than the typical John Day, *Eporeodon trigonocephalus* is advanced to a horizon, which is nearer contemporaneity with *Phenacocælus*; (See Amer. Jour. Sci., 1921, (5) Vol. 2, p. 951).



of the canal for the vertebral artery, which perforates the base of the transverse process; (8) by relatively lighter cervical vertebræ, due to the relatively smaller head; (9) by the relatively greater antero-posterior and smaller transverse diameter of the neural spines of the anterior dorsal vertebræ; (10) by a much less developed tubercle for the attachment of the internal humeral part of the triceps on the olecranon process of the ulna; (11) by a relatively shorter and heavier tibia, different shape of its shaft; (12) by having a shorter and broader hind foot.

#### THE SYSTEMATIC POSITION OF PHENACOCÆLUS.

From the foregoing discussion it is safe to assume that *Phenacocælus* is a member of the extinct North American family *Agriochæridæ*. At the present time it is, however, difficult to point out the phylogenetic ancestry of *Phenacocælus* with any degree of certainty. In many respects the Oligocene genus *Merycoidodon* is sufficiently closely related to be regarded as in the line leading to *Phenacocælus*. For instance: the dentition, the short face, and elongated cranium, the large thoracic cavity and the general structure of the limbs and feet of *Merycoidodon* are characters very like those shown in *Phenacocælus*. However, a critical and detailed comparison of the bony structure of these two genera points rather to parallelism than to direct phylogenetic relationship. In no species of *Merycoidodon* known to the writer have we any indication of such important features, which are found in *Phenacocælus*, as the fronto-nasal vacuities, the enlargement of the preorbital foramen, and especially the tendency toward the formation of facial vacuities,<sup>14</sup> the height of the carpus, the different details of the construction of the tibia, and the short hind foot. In the limbs and feet of *Phenacocælus* are important characters, which we are not now able to compare with genera and species imperfectly known from the lower Oligocene. The shortening of the hind foot in *Phenacocælus* seems to be more in line with the condition found in *Agriochærus* than in any other early genus now known. The enormously inflated tympanic bulla is analogous to that in *Agriochærus*, *Merycoidodon bullatus*, and *Limnenetes platyceps* of the early Oligocene Oreodonts. We may then conclude that the direct ancestral line of *Phenacocælus* had in the early Oligocene time established characters along an entirely independent line, paralleling such genera as *Agriochærus*, *Merycoidodon*, and *Limnenetes*. Nor should we forget that comparatively little field-work has been done in the way of collecting the smaller fossil remains in the basal Oligocene. When we consult such discriminatory work as

<sup>14</sup>In a recent publication (Amer. Jour. Sci., (5) Vol. II, 1921, p. 109) Thorpe describes *Paroreodon marshi* as having facial vacuities in advance of the orbits.

that of Leidy,<sup>15</sup> Douglass,<sup>16</sup> Loomis,<sup>17</sup> and others it becomes quite patent that we may yet find Oreodonts somewhere in the basal horizons of the Oligocene which probably will furnish just such anatomical points as we may expect to discover in forms ancestral to *Phenacocælus* and *Leptauchenia*.

*Phenacocælus* and the phylum of *Leptauchenia*-*Cyclopidius* have no especially close relationship, but parallel one another more closely. This is indicated by the many cranial similarities; *i. e.*, the fronto-nasal vacuities, the position of the orbit, the size of the tympanic bulla, &c., together with other features, namely: the numerical identity of the vertebral formula, the large thoracic and pelvic cavities. The limbs and feet of *Leptauchenia* are on the whole more like those of *Merycoidodon* than of *Phenacocælus*. One prominent feature of the fore limb in *Leptauchenia* is the great development of the antero-internal angle of the proximal end of the olecranon process of the ulna. This tubercle indicates a strong attachment for a branch of the extensor muscles of the fore arm, which is not nearly as well indicated in *Phenacocælus*, or any other known Oreodont.

The aquatic habit of *Leptauchenia* and *Cyclopidius* advocated by Professor Cope (Proc. Amer. Philos. Soc., XXI, 1884, p. 547) appear to be doubted by Dr. Sinclair, for the reason that the construction of the feet is apparently for cursorial habit on firm ground, and Sinclair disagrees with Cope in regarding the skull as pointing toward aquatic life on part of the animal. Sinclair believes that the geological formation in which *Leptauchenia* is found (heavy bedded clays) is a safer clue to the habit of the creature than the structure of its skeleton<sup>18</sup> (*op. cit.*, XLIX, 1910, p. 198).

Many features displayed in the osteology of *Phenacocælus*, especially those of the cranium, point to relationship with *Leptauchenia* and *Cyclopidius*, but the specialization of the latter genera shows, on the whole, a greater separation from the earlier types of the family than is the case in *Phenacocælus*.

The *Leptauchenia*-like features of the cranium in *Phenacocælus* possibly

<sup>15</sup>"The Extinct Mammalian Fauna of Dakota and Nebraska." Jour. Acad. Nat. Sci., Vol. VII, 1869, pp. 104-106. Leidy describes three species: "*Oreodon*" *affinis*, "*O*" *hybridus*, and "*O*" *bullatus* supposed to be from the lower Oligocene of Nebraska and Dakota.

<sup>16</sup>Trans. Amer. Philos. Soc., Vol. XX, 1901, pp. 260, 262. Douglass describes *Limnenetes platyceps* and *L. anceps* from the basal Oligocene of Montana.

<sup>17</sup>Ann. Car. Mus. Vol. XV, 1924, p. 370-373. Loomis erects *Oronetes* as a genus using the type of *Limnenetes anceps* Douglass and associated material in the Carnegie Museum as the basis of his description.

<sup>18</sup>Thorpe in a recent publication (Jour. Mammalogy, VI, No. 2, May, 1925, p. 73) follows Cope in advancing the idea that *Leptauchenia* was aquatic from the peculiar position of the eye, ear, and other features of the skull.



suggest the same mode of life as that of *Leptauchenia*, whatever it was, while the limbs, especially the hind limb, are of a decidedly heavier type and the hind foot is relatively shorter, which plainly indicates an animal having less speed than the *Leptauchenia* and perhaps more closely confined to denser vegetation, as a means of protection.

#### POSTSCRIPT.

Since the manuscript of the foregoing paper was prepared in 1909 and revised in 1914, much work has been done on the Oreodonts. Loomis of Amherst and Thorpe of the Peabody Museum, have contributed a great many papers from time to time. A study by Loomis of the cranial, and especially the dental structure of the premolars of the Artiodactyla in general, and the Oreodontidæ in particular, resulted in the division of that family into five distinct phylogenetic groups. While it is true that the axial skeleton (excepting the skull) and the appendicular skeleton of the Oreodonts from the earliest to the latest forms, are all quite generalized in character, we learn from careful detailed study of complete skeletal material that there are definite characters, which together with those of the cranium, may prove of greater value in phyletic study than is now generally admitted. From the comparative study of the three genera, *Merycoidodon*, *Phenacocælus*, and *Leptauchenia*, with which the foregoing pages chiefly deal, there is for instance revealed the fact that *Phenacocælus* had the hind limbs, especially the hind feet, more nearly like those of *Agriochærus* than any other Oreodont, of which those parts are known, and would no doubt be placed in phylogenetic relationship with that genus, if no other parts of its structure were known. Loomis (*l. c.* p. 15) places *Phenacocælus* in the line of more direct descent from *Eporeodon*, and also advances the idea that *Phenacocælus* belongs to the line of *Ticholeptus* because of the relatively slight change in the structure of the teeth.<sup>19</sup> While my limited comparative study of the Oreodonts does not at this time warrant proposing any change in Dr. Loomis' proposed scheme, I, however, am undisturbed in my views as to the systematic position of *Phenacocælus*, which I reached, many years ago. When the full description of the skeleton of *Eporeodon socialis*, promised by Thorpe<sup>20</sup> appears; when we know more fully the skeletal structure of other species of *Eporeodon*, as well as of other genera from the John Day and the upper Oligocene; when we get more complete information than is furnished by Thorpe<sup>21</sup>, on the extensive material

<sup>19</sup>Bull. Amer. Mus. Nat. Hist., Vol. LI, p. 12, 1924.

<sup>20</sup>Amer. Journal Science, (5) Vol. VII, 1924, p. 224.

<sup>21</sup>Ibid. Vol. II, December 1921, p. 339.



of *Merycoidodon affinis* in the Yale Museum; when we have more complete knowledge of the genera of this family already found in the basal Oligocene, and others, perhaps yet to be discovered somewhere in the lower horizons of the Oligocene, we shall be in possession of much needed and welcome information in support, or non-support, of our hypothesis and guesses in connection with the phylogeny of the Oreodontidæ.



## EXPLANATION OF PLATE XVI.

All figures from 1 to 39 inclusive are from the type specimen of *Phenacocælus typus* No. 1263, except figure 31 which is a view of the paratype of *Phenacocælus typus* No. 1335.

Figs. 1-7. Views of cervical vertebræ, left side.

Fig. 8. Dorsal view of atlas.

Fig. 9. Ventral view of atlas.

Figs. 10-29. Views of vertebral column from the first dorsal to and including a portion of the first sacral in their relative order of sequence; seen from the left side.

Fig. 30. Views of anterior caudal vertebræ; left side.

Fig. 31. Skull and lower jaws of *Phenacocælus typus*; paratype No. 1335. View of right side.

Fig. 32. Scapula; external face.

Fig. 33. Humerus; anterior face.

Fig. 34. Radius and ulna; anterior face.

Fig. 35. Fifth and sixth lumbar vertebræ and a portion of the first sacral vertebra as found in position; view from above.

Fig. 36. Right side of pelvis.

Fig. 37. Left tibia; anterior face.

Fig. 38. Left tibia and fibula; anterior face.

Fig. 39. Left tibia and fibula; fibular face.

All figures one-half natural size.





For explanation see opposite page.



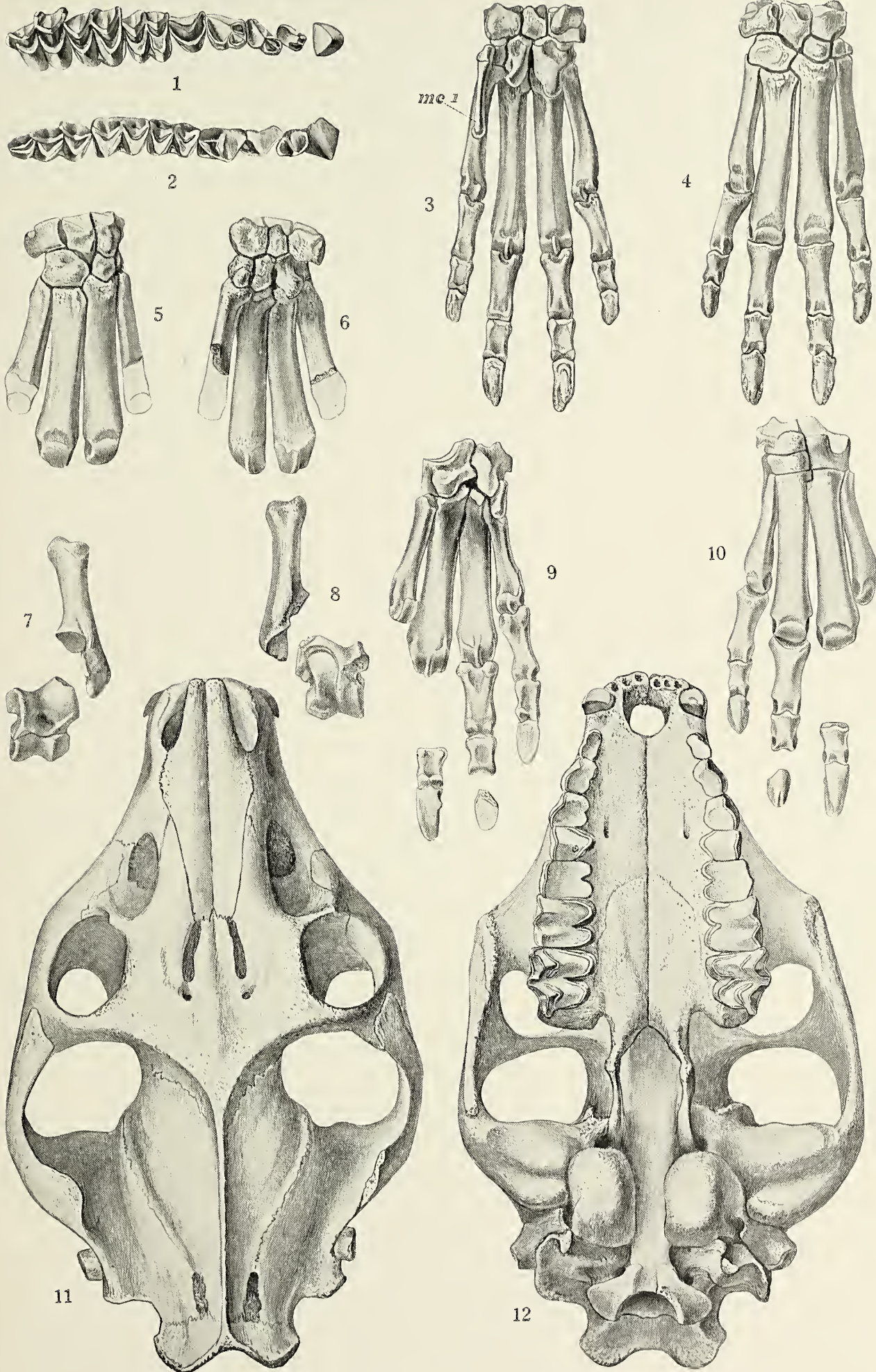




## EXPLANATION OF PLATE XVII.

- Fig. 1. Upper cheek-teeth, *Phenacocælus typus*, paratype No. 1335.  
Fig. 2. Lower cheek-teeth, *Phenacocælus typus*, paratype No. 1335.  
Fig. 3. Palmar face of right manus, *Merycoidodon culbertsoni*, No. 1391.  
Fig. 4. Dorsal face of right manus, *Merycoidodon culbertsoni*.  
Fig. 5. Dorsal face of right manus, *Phenacocælus typus*, No. 1263.  
Fig. 6. Palmar face of right manus, *Phenacocælus typus*, No. 1263.  
Fig. 7. Left calcaneum and astragalus, dorsal face, *Phenacocælus typus*, No. 1263.  
Fig. 8. Left calcaneum and astragalus, plantar face, *Phenacocælus typus*, No. 1263.  
Fig. 9. Plantar face of pes, *Phenacocælus typus*, No. 1263.  
Fig. 10. Dorsal face of pes, *Phenacocælus typus*, No. 1263.  
Fig. 11. Top of skull, *Phenacocælus typus*, paratype No. 1276.  
Fig. 12. Palatal view of skull, *Phenacocælus typus*, paratype No. 1276.

All figures two-thirds of nature.



For explanation see opposite page.



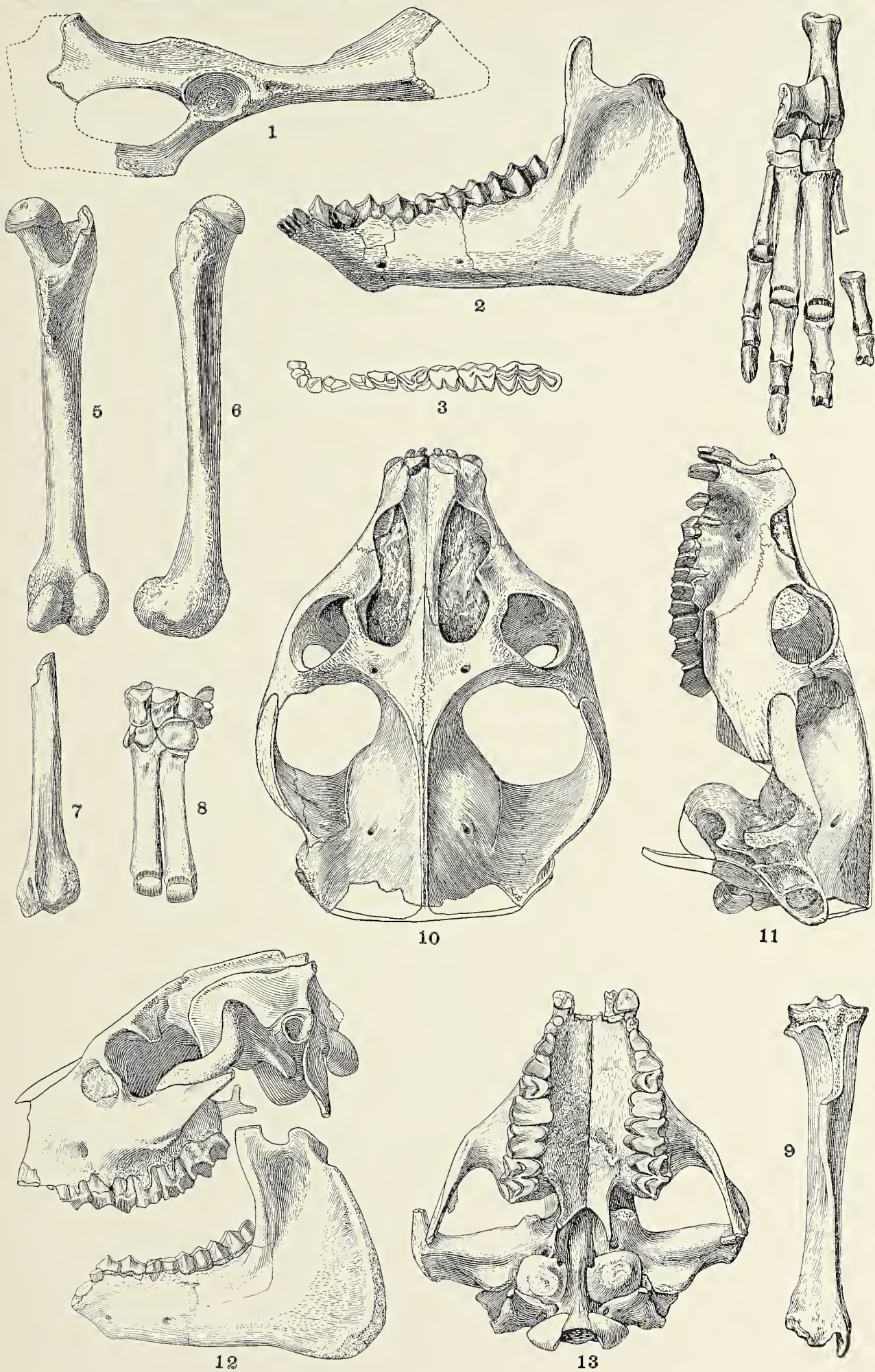




## EXPLANATION OF PLATE XVIII.

- Fig. 1. Portion of right side of pelvis, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 2. Left lower jaw, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 3. Lower dentition in outline, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 4. Dorsal face of pes, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 5. Posterior face of femur, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 6. Fibular face of femur, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 7. Anterior face of radius, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 8. Dorsal face of manus, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 9. Anterior face of right tibia, *Phenacocalus munroënsis*, type No. 1288.  
Fig. 10. Top view of skull, *Cyclopidius* No. 1307.  
Fig. 11. Side view of skull, *Cyclopidius*, No. 1307.  
Fig. 12. Skull and jaws, view of left side, *Phenacocalus typus*, paratype, No. 1278.  
Fig. 13. Palatal view of skull, *Phenacocalus typus*, paratype, No. 1278.

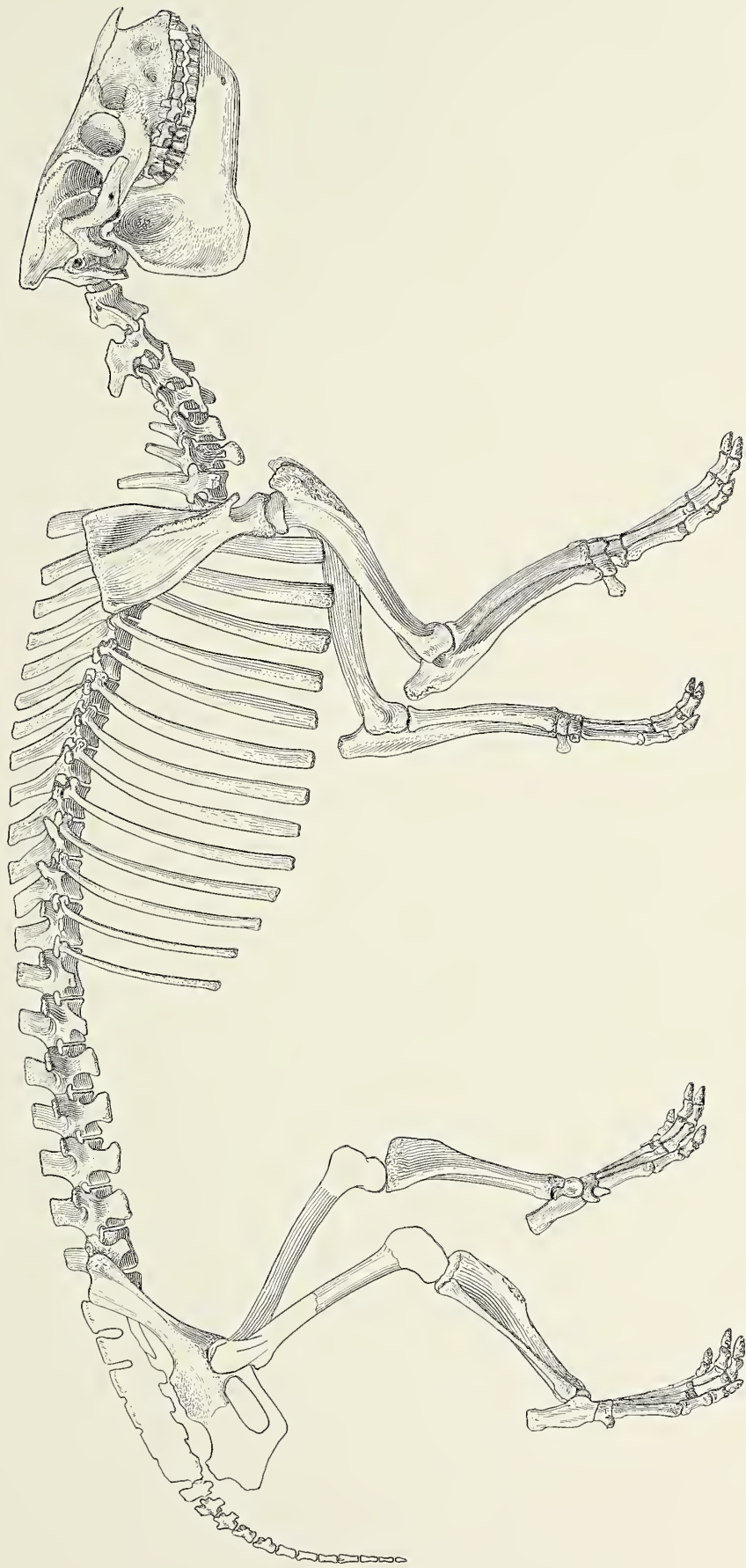
All figures one-half of nature, except figure 10 and 11 which are natural size.



For explanation see opposite page.







Articulated Skeleton of *Phenacocetus typus* Peterson.  
Type of the genus and species (C. M. Cat. Vert. Foss., No. 1263). One-fourth natural size.







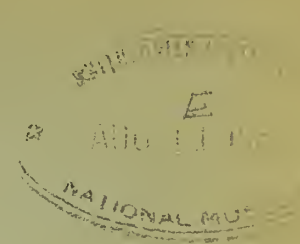
*Phenacocoelus typus* Peterson.

Restoration of the Type of the Genus (C. M. Cat. Vert. Foss., No. 1263). One-sixth natural size.





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MEMOIRS  
OF THE  
CARNEGIE MUSEUM

VOL. XI

No. 4

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OSTEOLOGY OF APATOSAURUS, WITH SPECIAL REFERENCE TO  
SPECIMENS IN THE CARNEGIE MUSEUM

By CHARLES W. GILMORE  
Curator of Vertebrate Paleontology, U. S. National Museum

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PITTSBURGH  
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OSTEOLOGY OF APATOSAURUS,  
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U. S. National Museum

## DEDICATION

This comprehensive work is dedicated to the memory of Dr. William Jacob Holland, whose enthusiasm for paleontology was among the many preoccupations of his long, busy, and eminently productive life. Sometime before his lamented passing away he made all necessary provision for producing a monograph such as this on the great Dinosaur named in honor of Mrs. Andrew Carnegie, but did not see this dream fulfilled in the span of his lifetime. May this treatise serve as a reminder to the scientific world of the exceptional breadth of interests which inspired the late scholar.

A. AVINOFF,  
*Director*









Life restoration of *Apatosaurus lousiae* Holland, drawn by Dr. A. Avinoff.  
(Memoirs, Carnegie Museum, Vol. XI. To face p. 175)



# MEMOIRS OF THE CARNEGIE MUSEUM

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## INTRODUCTION

The Carnegie Museum enjoys the distinction of having the most extensive collection of sauropodous dinosaur remains ever assembled. In number of articulated skeletons, and general excellence of their preservation, the collection is unrivaled. The bringing together of such a collection of fossil vertebrates entails the expenditure of a considerable sum of money, and also a vast amount of energy, skill, and perseverance on the part of those to whom the work is entrusted, whether they be curators, preparators or collectors. The above observation applies to all fossil collections, but is particularly applicable to the present assemblage of dinosaurian skeletons composed as it is of the largest of all land vertebrates.

Several specimens of this collection have formed the basis of important monographic studies, contributing greatly to our knowledge of these huge reptiles; many more still remain in storage in the cases as they were received from the field.

It is the plan of the Director, Dr. A. Avinoff, to make this huge collection available to scientific and kindred institutions as expeditiously as can be arranged. First, by a well conceived series of monographic studies; second, by the exchange of duplicate specimens. In putting this plan into execution, Dr. Avinoff has invited me to make a study of an unusually perfect skeleton of *Apatosaurus*. This specimen was collected in 1909 and 1910 by parties working under the direction of the late Earl Douglass in the Dinosaur National Monument in northeastern Utah, and it was mounted for the exhibition series in 1913. It was the subject of preliminary study by the late Dr. William J. Holland,<sup>1</sup> who in a short paper designated it the type of the new species *Apatosaurus louisæ* named in honor of Mrs. Andrew Carnegie. It had long been Dr. Holland's intention to use this specimen as the basis for a memoir on the genus *Apatosaurus* and before death intervened, he had all of the bones of the skeleton illustrated, comprising some four hundred pen and ink drawings. All of these illustrations were made by the well known paleontological artist, Mr. Sydney Prentice, which accounts for the artistic merit as well as for the accuracy of the illustrations which adorn this paper.

At this time I wish to express my sincere appreciation to the members of the Paleontological Staff of the Carnegie Museum for the many courtesies extended me during the course of this investigation, and especially do I wish to acknowledge my great obligations to Dr. A. Avinoff, Director of the Carnegie Museum, for the opportunity given me to study these interesting specimens as well as his ever ready coöperation in all matters pertaining to the preparation and publication of this extended study.

<sup>1</sup>Holland, W. J., *Annals of the Carnegie Museum*, vol. X, Art. 10, 1915, pp. 143-145.

## THE DINOSAUR NATIONAL MONUMENT

The Dinosaur National Monument located in northeastern Utah, in the Uinta Basin some five and a half miles north of the little town of Jensen, see fig. 2, is one of the most remarkable dinosaur fossil deposits ever found. Since the specimen forming the basis of the present paper was in a way responsible for its exploration and development, it seems peculiarly appropriate at this time to give here a complete account of the operations carried on there.

The history of the Dinosaur National Monument, which was first designated the "Carnegie Museum Dinosaur Quarry," had its beginning in 1909 with the discovery of the *Apatosaurus louisæ* skeleton by Mr. Earl Douglass of the Carnegie Museum staff. Acting on a suggestion made by the late O. A. Peterson, who as early as 1892, while collecting fossils for the American Museum of Natural History, had found some fragmentary dinosaurian bones in the vicinity of Jensen on Green River, Mr. Douglass left the Eocene in the Uinta Basin where he had been collecting mammals and proceeded to explore exposures of the nearby Morrison formation. Although at first much discouraged, on August 19, 1909, at an elevation of about 5,000 feet above sea level, he discovered an articulated series of caudal vertebræ embedded in a sandstone ledge, see Pl. XXI, fig. 1. Returning on September 1st with a force of men, the excavation of the vertebræ was commenced. This specimen designated by the quarry number, "No. 1," turned out to be a very complete skeleton, and in excavating it other specimens were encountered, one after another, and thus the work continued for thirteen years. Although the deposit was not exhausted, work was discontinued here by the Carnegie Museum on December 31, 1922.

In the early work permits were secured from year to year from the Secretary of the Interior to carry on the explorations. Some years later, however, as Holland<sup>2</sup> observes: "To avoid being made to pay tribute to some adventurer, who might see fit to file a claim to the barren acres upon which we were carrying on our work, I instructed Douglass to file a claim under the existing laws." The decision that "fossil bones" mentioned by Douglass in his application were not mineral, the request for title to the land was disallowed. On October 4, 1915, however, under a law known as "An Act for the Preservation of American Antiquities," President Wilson, by presidential proclamation, set aside an area of 80 acres to be known as the Dinosaur National Monument and placed it under the jurisdiction of the National Park Service.

In the thirteen consecutive years that collecting was carried on here by Car-

<sup>2</sup>Holland, W. J., Memoirs of the Carnegie Museum, vol. IX, no. 1, p. 383, 1922.



negie Museum parties, a great mass of materials, some 700,000 pounds in all, was shipped to the Museum in Pittsburgh. In these collections were articulated skeletons of both large and small dinosaurs, and especially important was the recovery of a considerable number of well preserved skulls, the rarest and most sought-for part of the dinosaurian skeleton. The diversity of forms represented, the perfectness of their preservation and their great abundance, marks this as one of the richest deposits of Morrison fossils ever discovered.

In order to preserve all of the evidence of the original association of the skeletons and scattered bones, which later might be of assistance in assembling disarticulated parts when the specimens should be prepared in the Museum laboratory, Douglass had a quarry map prepared, see Pl. XXIII, on which all specimens as they were uncovered, were plotted. In order to insure the accuracy of the map, the quarry was marked out in four foot squares, see Pl. XXI, fig. 2, and whatever bones were found within the limits of one of these squares was sketched in a corresponding square on the quarry map, reduced to a scale of one-half inch to the foot. The map resulting, see Pl. XXIII, was largely the work of Mr. J. LeRoy Kay, assistant to Douglass, and he is to be highly complimented in having successfully accomplished so difficult an assignment. The quarry map here reproduced for the first time presents an accurate picture of the relative relationships of the skeletons and skeletal parts as they were originally found in the sandstone. Some of the skeletons are essentially complete, but more frequently only portions were found such as a tail, a section of the back, a neck, or a complete limb or foot.

A study of the quarry map shows the skeletons and bones to be grouped in large clusters, with intervals between, where fossils are sparse and few articulated parts are found. This appears to indicate that once a large carcass had stranded it formed a barrier to the current causing a diversion of the stream, which in passing around cut new channels and further scattered and disarticulated any skeletal parts encountered. The change in direction of the long bones on the outer margins of these clusters indicates the course of the currents. It is very evident that the main current of the stream ran from west to east. The long tails of the Sauropod dinosaurs, like streaming water plants in a river, have a similar down stream, eastward course. Furthermore, when parts of a skeleton are found detached and shifted out of position they have in most instances been found to the eastward of the main portion of the skeleton.

The character of the sediments indicates that apparently this represents the area of a series of old river bars, which in their shallow waters arrested the more or less decomposed carcasses, collected from many points upstream, perhaps during freshets. Thus were brought together here the animals of a whole region, a fact

which vastly enhances the interest of this great deposit. The final part of the story necessitates a rapid covering of the stranded carcasses by sand and other river sediments in order that the bones of the skeletons should become fixed in their relative positions before decomposition of the ligamentary attachments allowed them to shift out of position. That many of the larger skeletons were not completely covered immediately is shown by the fact that while the bones of the lower side remain undisturbed, those of the upper often show much displacement of parts. The strong cross-bedding of the sandstones, and the assorting of the coarse and fine materials of which the sandstones are composed give further evidence of the currents that swirled and eddied around these stranded carcasses.

In this quarry a veritable "Noah's Ark" of the animals of the Morrison period has been found. Here were skeletons of the largest of the giant Sauropodous dinosaurs, closely intermingled with remains of the smaller but powerful flesh-eating forms, and those of the slow heavily armored *Stegosaurus*, as well as the smallest and most bird-like dinosaurs.

Intermingled with these are an occasional turtle shell of the genus *Glyptops*, crocodile remains, fresh water shells, cycads, and fossil leaves, and wood fragments.

The complete faunal list of the Dinosaur National Monument Quarry, as known at the present time, is as follows:

Dinosauria

Saurischia

*Apatosaurus louisæ* Holland

*Barosaurus* sp.

*Camarasaurus lentus* (Marsh)

*Camarasaurus* sp.

*Diplodocus longus* Marsh

*Pleurocoelus* sp.

*Uintasaurus douglassi* Holland

*Antrodemus* (*Allosaurus*) sp.

Ornithischia

*Camptosaurus medius* Marsh

*Dryosaurus altus* Marsh

*Laosaurus gracilis* Marsh

*Stegosaurus* sp.

Crocodyliformi

*Goniopholis* sp.



## Chelonia

*Glyptops utahensis* Gilmore

## Phytosauromorphi

*Hoplosuchus kayi* Gilmore

During the thirteen years that the Carnegie Museum parties explored this deposit for fossils, the work, from first to last, was under the direction of Mr. Earl Douglass. In that period he was assisted by the men whose names follow, all of whom at that time were residents of the state of Utah: Joseph Ainge, Earl Douglass, J. A. Kay, J. LeRoy Kay, J. T. Kay, Clarence Nielson, Francis Schuler, William Schafermeyer, R. C. Thorne, E. M. York, Golden York.

To bring the history of the Dinosaur National Monument up to the present, mention should be made of the work done there by the U. S. National Museum and the University of Utah following its abandonment by the Carnegie Museum. In the final work of the Carnegie Museum collectors, two articulated sauropod dinosaur skeletons were partially uncovered. This fact was communicated to the officials of the Smithsonian Institution by the late director of the Carnegie Museum, Dr. Douglas Stewart, and steps were immediately taken to resume work here in order to secure a mountable skeleton of one of these huge reptiles for the National collection. It was my privilege to be placed in charge of the operations.

Arriving at the quarry about the middle of May 1923, a preliminary survey showed that of the two skeletons partially exposed in relief, the one bearing the field designation "No. 355," a *Diplodocus*, although lacking the neck, appeared to offer the best basis for an exhibition skeleton.

At that time it seemed to be beautifully supplemented by a second specimen, field No. 340, having an articulated cervical series, part of which had already been taken out by the Carnegie Museum collectors, and which later was generously turned over to the National Museum by Director Stewart. Later, preparation in the laboratory showed this neck to pertain to the genus *Barosaurus* and it could therefore not be used to replace the missing *Diplodocus* neck.

Regular work in the quarry was begun in the latter part of May and proceeded continuously up to August 8, in which time all of the *Diplodocus* specimen and such parts of the second individual as were needed were collected and shipped to Washington, D. C. Some 52,000 pounds of fossil bones and matrix were collected. Since then, the specimen has been prepared and mounted and it now forms one of the prominent exhibits in the hall of vertebrate paleontology of the United States National Museum.

Almost immediately after the cessation of work by the National Museum



collectors, the University of Utah commenced the excavation of the remaining part of the *Barosaurus* skeleton, a task successfully accomplished under the direction of Mr. Earl Douglass. A second well-preserved skeleton of *Antrodemus* (*Allosaurus*) was also collected for that Institution.

No collecting has since been done there, although a project planned by the National Park Service is to develop a permanent exhibit of the fossils *in situ*. It is proposed to clear off a considerable area of the fossil-bearing sandstone and chisel the contained fossils out in bold relief, over which will be erected a suitable building for their protection and thus develop here a unique exhibition typical of the monument. Nowhere else do the natural conditions permit of so realistic a display of dinosaurian remains in their original environment. The steep tilting of the fossil-bearing strata and the abundance of articulated skeletons are both features assuring the success of the undertaking. It is anticipated that when finished it will form one of the outstanding points of interest to those tourists who visit our National Parks.

#### GEOLOGY OF THE DINOSAUR NATIONAL MONUMENT QUARRY.

The principal dinosaur-bearing layer is a heavy, greenish, conglomeratic, cross-bedded sandstone that occurs in the upper half of the Morrison formation. The whole geological section, see fig. 1, beginning with the Palæozoic and extending upward successively through the Triassic, marine Sundance, Morrison, Dakota?, Aspen shale, and Frontier formations is steeply tilted with a dip of  $60^\circ$  to the south. Although dinosaur bones have been found at other levels, nowhere are they so abundant or so well preserved as in the ten-foot sandstone mentioned above. The outcropping ledge formed by this layer of fossil-bearing sandstone,

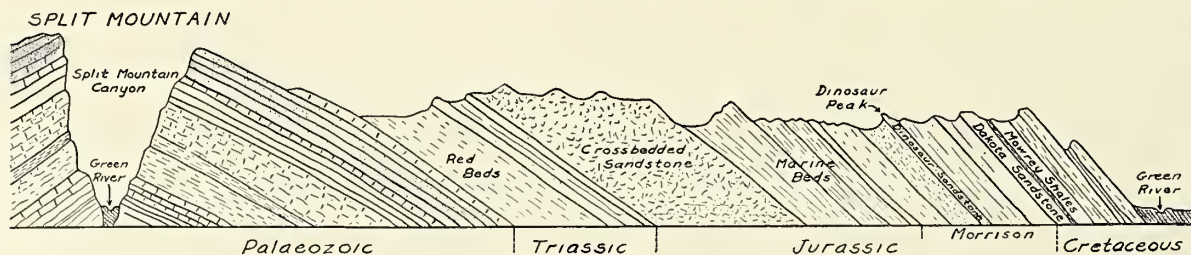


FIG. 1. Geological section near Dinosaur National Monument, Uinta County, Utah.

which weathers brown, can be easily traced for considerable distances both east and west of the hogback where the quarry is located and fossil remains are evident almost everywhere.

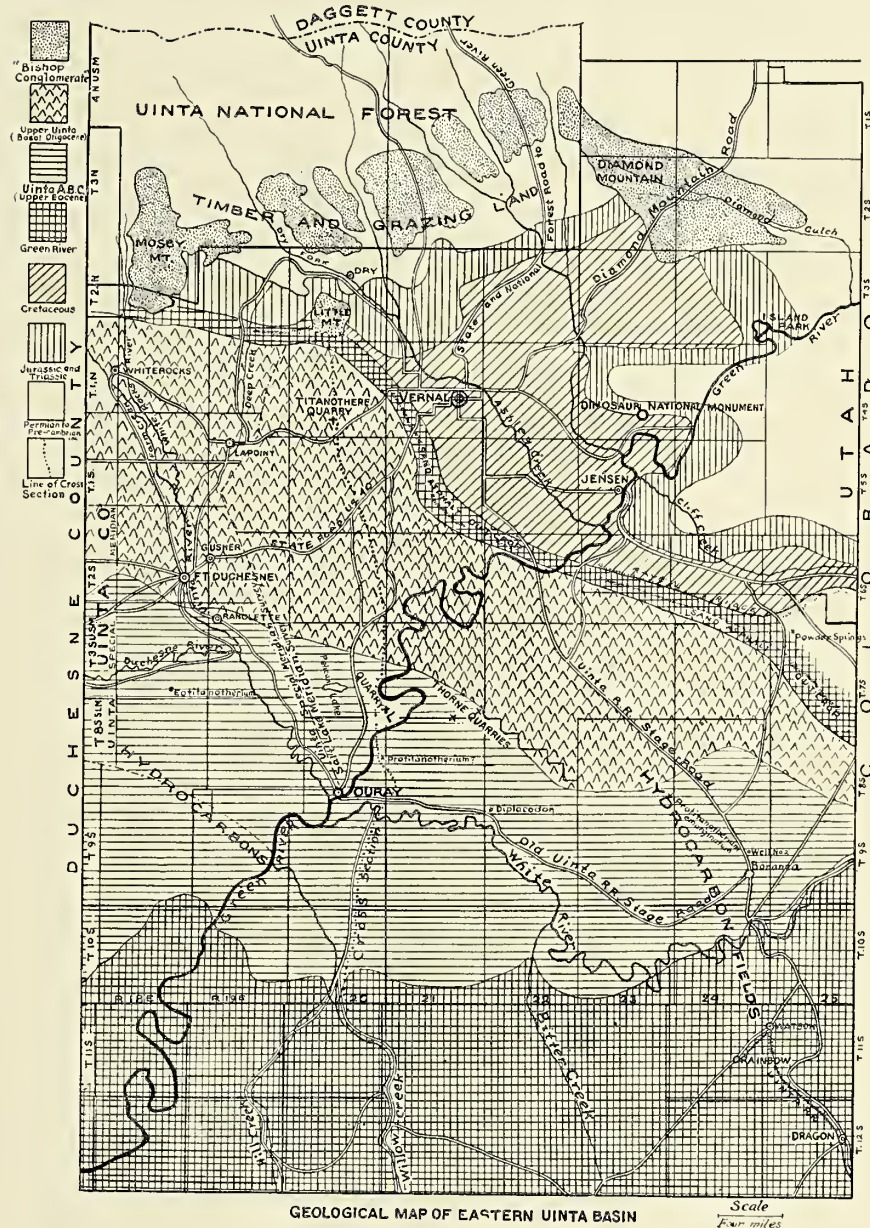


FIG. 2. Geologic map, showing the geology and geographic location of the Dinosaur National Monument. After Peterson and Kay.

The Morrison in this locality is composed lithologically of alternating beds of sandstones and shales of varying thicknesses, the whole formation in this section having a total thickness of 795 feet. The following section was measured by Dr. John B. Reeside, Jr.,<sup>3</sup> in 1922 in the neighborhood of the quarry.

<sup>3</sup>Reeside, J. B., Jr., Prof. Paper 132-C, U. S. Geol. Surv., 1923, p. 44.



## SECTION MEASURED AT DINOSAUR NATIONAL MONUMENT QUARRY

		FEET
CRETACEOUS	River-terrace materials, underlain by Hilliard shale . . . . .	...
	Frontier formation:	
	Sandstone, fairly coarse, gray to brown, cross-bedded . . . . .	22
	Shale, yellow, sandy, with thin layers of gray sandstone . . . . .	158
	Aspen shale:	
	Shale, bluish-gray, contains many fish scales . . . . .	50
	Shale, yellowish, sandy . . . . .	37
	Dakota? sandstone:	
	Sandstone, gray to brown, locally weathering pink, conglomeratic, cross-bedded . . . . .	35
	Shale, rusty brown and drab . . . . .	27
	Sandstone, gray to brown, in thin beds . . . . .	10
	Shale, rusty brown and drab . . . . .	37
	Sandstone, ripple-marked, brown to gray, cross-bedded . . . . .	37
JURASSIC	Morrison formation:	
	Shale, gray, violet and greenish, with lenses of greenish argillaceous sandstone, grit, and conglomerate, that weather to a chocolate-brown; highly variable unit . . . . .	279
	Sandstone, greenish, conglomeratic; weathers brown.	
	Horizon of dinosaur quarry . . . . .	10
	Shales and sandstone, variegated; like second unit above . . . . .	506
	Sundance formation:	
	Sandstone, fine grained, fissile, beautifully ripple-marked and rain-pitted, greenish-gray, with interbedded shale. Some layers contain <i>Ostrea</i> sp. . . . .	40
	Sandstone, platy, ripple-marked, gray, fine grained; contains <i>Rhynchonella gnathophora</i> Meek, and <i>Tancredia warrenana</i> M. & H. . . . .	2
	Shale, greenish-gray, with some platy sandstone, same color . . . . .	65
	Sandstone, brown, limy, contains <i>Ostrea strigilecula</i> . . . . .	1
	Shale, dark gray, almost black, containing dense blue limestone in concretions . . . . .	42
	Limestone, gray, coarse, sandy, contains <i>Eumicrotia curta</i> (Hall), <i>Ostrea strigilecula</i> White, <i>Camptoneustes platessiformis</i> White, <i>Astarte pachardi</i> White, <i>Tancredia? inornata</i> Meek and Hayden, <i>Tancredia</i> sp., <i>Dosiniajurassica</i> Whitfield?, <i>Cardioceras russelli</i> Reeside, <i>Cardioceras hyatti</i> Reeside, <i>Cardioceras cordiformis</i> Meek and Hayden, <i>Cardioceras</i> aff. <i>C. wyomingense</i> Reeside, <i>Cardioceras</i> sp. . . . .	1
	Shale, greenish-gray, with limestone in nodules and containing <i>Ostrea strigilecula</i> White, <i>Eumicrotis curta</i> Hall . . . . .	27
TRIASSIC	Nugget sandstone of authors:	
	Sandstone, massive, cross-bedded, yellow to gray . . . . .	91
	Shale, and platy sandstone, yellow to gray . . . . .	12
	Sandstone, massive, gray to yellow, cross-bedded . . . . .	120
	Shale, variegated, gray to brick red . . . . .	107
	Sandstone, very massive, yellow to gray, forms here an impassable ridge, must be some hundreds of feet thick.	



POSITION OF THE *APATOSAURUS LOUISÆ*  
SKELETON IN THE QUARRY

Specimen No. 3018 C. M. in its present articulated condition, is a remarkably complete Sauropod skeleton, but when found in the quarry it was in much disarray, as shown in fig. 3. The vertebral column, which is completely preserved from the atlas to the sixty-fourth caudal vertebra was found separated into three main segments, with a further disarrangement of the distal caudals as shown in fig. 3. The complete cervical series of fifteen vertebræ was turned backward above the articulated dorsal section, the anterior members lying under the articulated pelvis. The dorsal segment had been turned over and lay on its left side, shifted some three or four feet out of line with the sacrum and the articulated caudal series. Excepting the first dorsal, which had become disarticulated and lay on its anterior face, all the others were articulated by their zygapophyses. The sacrum with the attached ilia, pubes, and ischia, formed a continuous articulated series as far back as the twenty-sixth caudal. From this point, posteriorly, there were intervals of disarrangement, but the more or less continuous line of vertebræ of diminishing size leaves no doubt of their having pertained to a single individual. When assembled for mounting, the gradation in size was so regular as to indicate a continuous series and they have been so arranged in the mounted skeleton.

The right femur was not articulated in the acetabulum as mistakenly stated by Doctor Holland,<sup>4</sup> but as shown by the original quarry map, it, with the tibia, fibula, and astragalus, lay in the interspace between the cervical and dorsal segments.

The articulated left fore limb and foot had been shifted to the east and south of the main mass of the skeleton. Of the right fore limb only the humerus, scapula, and coracoid were recovered. These bones were widely scattered as shown in the accompanying diagram. The left hind foot was found in an isolated position considerably above the cervical series. None of the eighteen thoracic ribs recovered were found articulated but were intimately intermingled with the other parts of the skeleton as shown in fig. 3.

The accompanying diagram has been re-drawn from the original quarry map made at the time of collecting the specimen with some refinements added as the contents of the blocks of matrix were revealed by the preparators in the laboratory. Since all surrounding skeletons and miscellaneous bones have been omitted, it gives a clearer conception of the skeleton as it was originally found.

It was the finding of the articulated caudals (11 to 20) protruding from the

<sup>4</sup>Holland, W. J., *Annals Carnegie Museum*, vol. X, Art. X, 1915, p. 1.

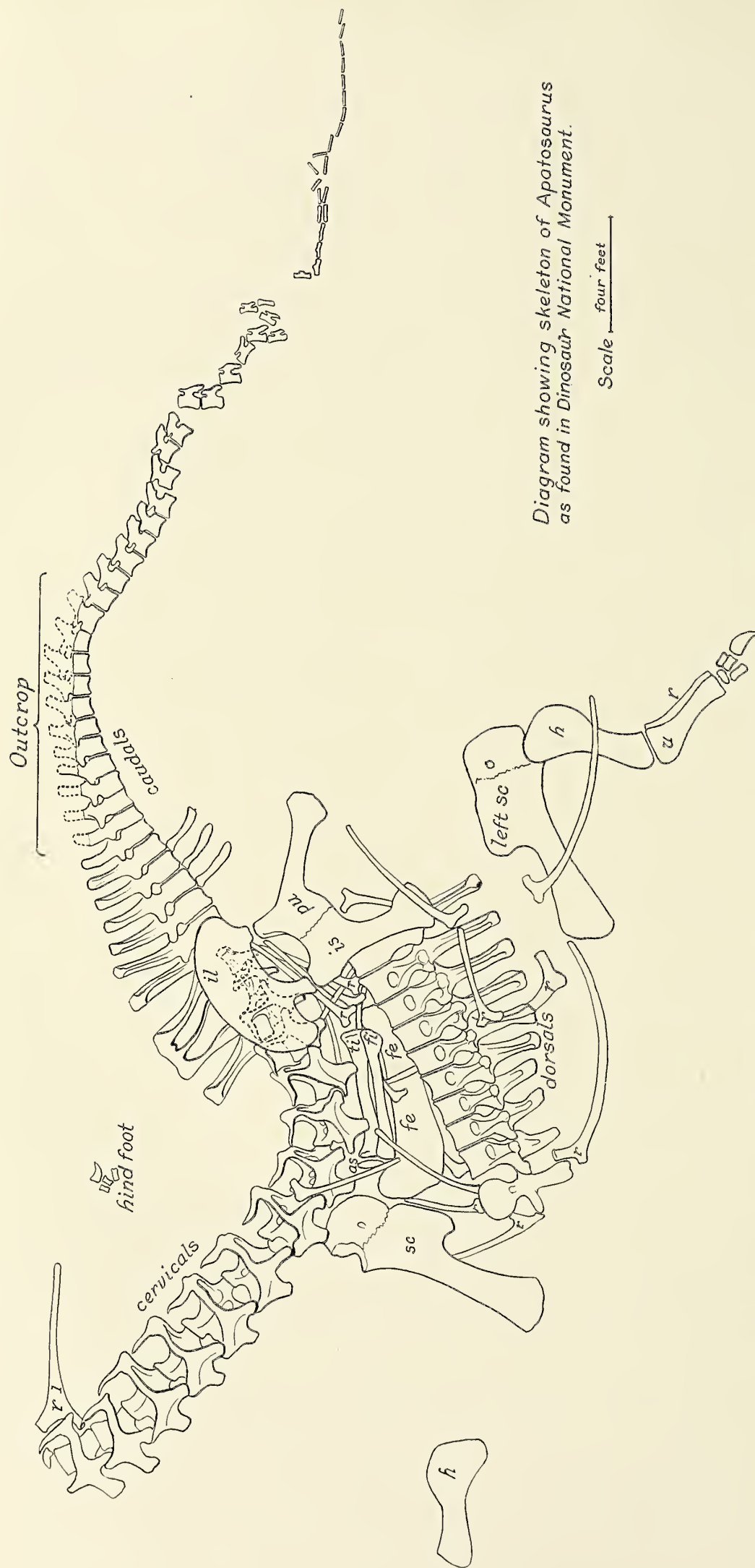


Diagram showing skeleton of *Apatosaurus*  
as found in Dinosaur National Monument.

Scale four feet

FIG. 3. Diagram showing the relationships of the various parts of the skeleton of *Apatosaurus louisei* Holland as found in the sandstone. *As*, astragalus; *fe*, femur; *fi*, fibula; *h*, humerus; *il*, ilium; *is*, ischium; *r*, ribs; *r1*, first dorsal rib; *r*, ribs and radius; *sc*, scapula; *ti*, tibia; *u*, ulna; *outcrop*, indicates the portion that was protruding from the rock, and which led to its discovery.



ledge of rock which led to the development of this unrivaled deposit of fossils. The initial discovery is clearly shown in Pl. XXI, fig. 1, reproduced from a photograph taken at the time by Mr. Earl Douglass.

A detailed list of the skeletal parts recovered is as follows: 15 cervicals, 10 dorsals, 5 sacral and 64 caudal vertebræ; 20 cervical ribs; 18 thoracic ribs; 3 anterior chevrons; both ilia; both pubes; both ischia; right femur, tibia, fibula, and astragalus; left pes, lacking metatarsal V and phalangeal 3 of digit II, 2 of digit III, and all of digit V; left scapula, coracoid, humerus, ulna, radius, scapho-lunar, and manus. The latter lacks proximal phalangeals of digits III, IV, and V. The right fore limb is represented by the scapula, coracoid, and humerus. The sternal bones were not recovered.

#### DETAILED DESCRIPTION OF THE SKELETON OF *APATOSAURUS LOUISÆ* HOLLAND.

*Apatosaurus louisæ* Holland, W. J., Ann. Carnegie Museum, X, 1915, pp. 143-145; Ann. Carnegie Museum, XV, 1924, p. 120, fig. 2; Mem. Carnegie Museum, IX, 1924, pp. 383, 386; Eastman, C. R., Amer. Year Book (1916) 1917, p. 656; Science (n.s.) 1917, p. 119; Gilmore, C. W., Mem. Carnegie Museum, X, 1925, p. 367; Proc. U. S. National Museum, 81, No. 2941, 1932, p. 6; Hay, O. P., Carnegie Instit. Wash., Pub. 390, II, 1929, p. 195; Huene, F. v., Eclogæ Geol. Helvetiæ, XX, 1927, p. 465; Monog. zur. Geol. und Paleont. Leipzig, Ser. I, IV, 1932, p. 288; Moodie, R. L., Palæopathology, University Press, 1923, p. 192, Pl. XXIX; Mook, C. C., Ann. N. Y. Acad. Sci., XVII, 1916, p. 140.

*Type*: No. 3018, C. M., consists of a fairly complete skeleton. Collected by Earl Douglass and party, 1909-1910.

*Locality*: Dinosaur National Monument, Uinta County, Utah.

*Horizon*: Morrison (Beckwith), Upper Jurassic.

#### THE SKULL.

Although the genus *Apatosaurus* (*Brontosaurus*) was among the first of the Sauropodous Dinosauria to be discovered in North America, in the more than half a century that has elapsed no definite information has been obtained, and doubt still exists as to the nature of the skull this animal possessed. During this period at least a score of more or less complete skeletons have been discovered, but in no instance has a skull been found in such association that it can be positively assigned to that genus.

For more than twenty years the mounted skeleton of *Apatosaurus louisæ* in the Carnegie Museum stood headless because of this lack of information. In a



paper<sup>5</sup> published in 1915, Dr. William J. Holland discussed this whole matter in considerable detail but without reaching any definite conclusion. The basis of his discussion rested upon two large skulls in the Carnegie Museum collection from the Dinosaur National Monument, both of which were found considerably removed from the *Apatosaurus* skeleton. Through a mistaken understanding he was led to say: "With this skeleton [No. 3018 C. M.] lying about twelve feet from the atlas, and in the same layer, was a skull the condyle of which shows perfect adaptation to the atlas." In this he was in error for Mr. J. LeRoy Kay, who was Douglass' assistant at the time these skulls were collected and who was largely responsible for the preparation of the quarry map shown in Pl. XXIII, informs me that this large Diplodocid-like skull, No. 11162 C. M., came from the western end of the quarry nearly 100 feet distant from the nearest bones of the *Apatosaurus* skeleton and in the lowermost part of the bone-bearing stratum. Likewise the second skull, No. 12020 C. M., discussed by Doctor Holland was found somewhat farther away, but higher up in the fossil-bearing strata at practically the same level as the *Apatosaurus* skeleton. These observations by Mr. Kay have been verified from the original records, so that the question of near proximity as an argument for the association of either of these skulls with the skeleton no longer obtains. The undoubted Diplodocid affinities of skull No. 11162 C. M., though it is larger than any *Diplodocus* cranium previously known, is sufficient in my estimation to exclude it from further consideration in this connection.

The second skull discussed by Doctor Holland, No. 12020 C. M. (see fig. 4), however, has the peculiar spoon-shaped dentition originally attributed to *Brontosaurus* by Professor Marsh, and its large size, and massiveness of structure appears in keeping with the general make-up of the *Apatosaurus* skeleton. That *Apatosaurus* had teeth of the kind mentioned is apparently indicated by the finding of a single tooth<sup>6</sup> of this character with the large *Apatosaurus* (*Brontosaurus*) skeleton now mounted in the American Museum of Natural History. This was an isolated specimen, that is, there was no mixture of other animal bones in the ground with this specimen and thus the inference would be that all of the elements including the tooth were of a single individual.

Careful study was made of the second incomplete skull (No. 12020 C. M.) discussed by Holland, in the hope it might be used to complete the mounted skele-

<sup>5</sup>Annals of Carnegie Museum, vol. IX, 1915, pp. 273-277.

<sup>6</sup>Recent correspondence with Dr. Walter Granger informs me that neither he nor Mr. Peter Kaisen, who assisted in the collecting of this specimen, has any recollection of the finding of a tooth but in a later conversation with Prof. R. S. Lull, who also assisted with this specimen, the latter assured me that he clearly remembers finding a spoon-shaped tooth in the quarry, and that he gave it to Dr. W. D. Matthew, but that the tooth was not seen afterward.



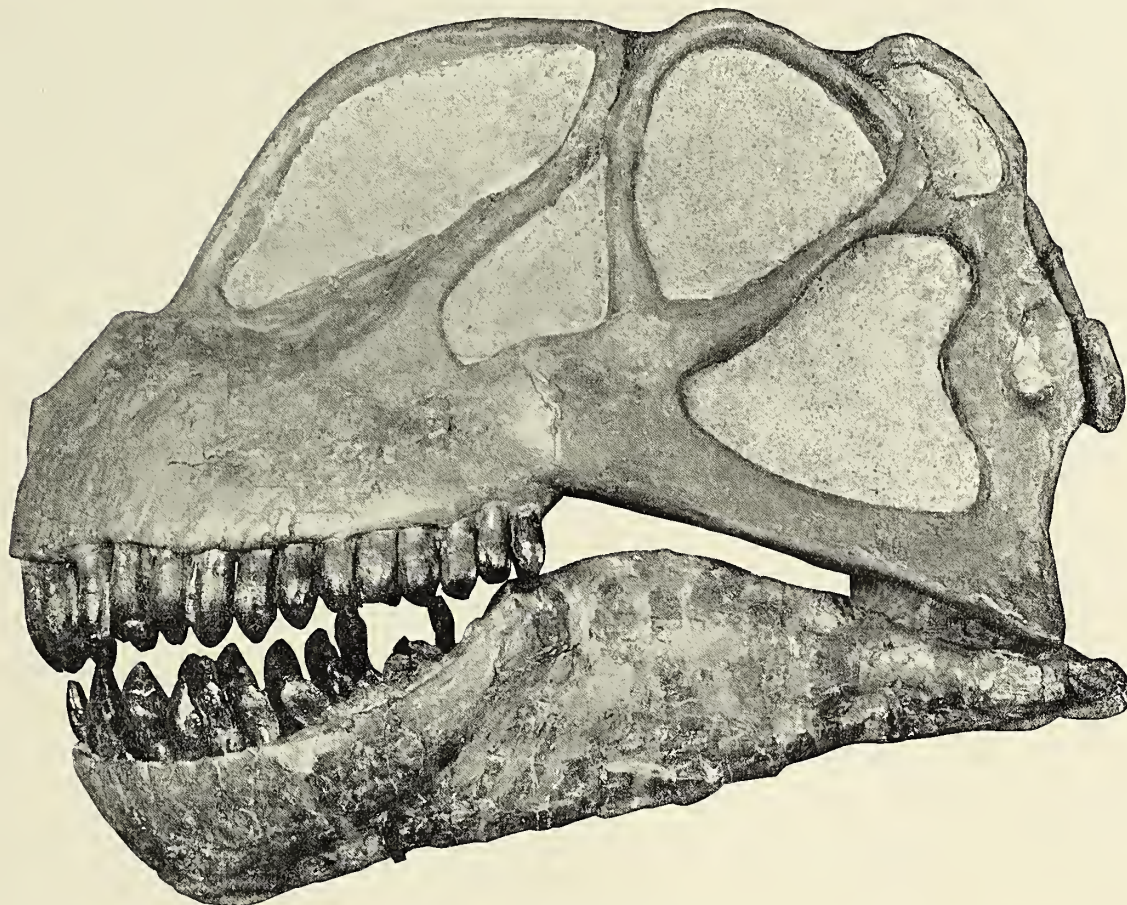


FIG. 4. Sauropod skull and lower jaws, No. 12020 C. M., a cast of which has been used to complete the mounted skeleton of *Apatosaurus louisæ*. About one-fifth natural size.

ton of *Apatosaurus louisæ*, but I was unable to satisfactorily distinguish it from the cranium of *Camarasaurus*, of which the Carnegie Museum possesses two smaller but beautifully preserved examples. Positive identification of this specimen was rendered difficult because of its incompleteness, as practically all of the top above the maxillaries is missing. Furthermore, when the skull came into my hands all of the original parts had been incorporated in a complete skull restoration, fig. 4, and thus all except the external surfaces of the bones were hidden from view. Practically all of the sutures were coalesced, and the bones surfaces are only fairly well preserved. It should also be mentioned that this skull was found in the quarry, see Pl. XXIII, intermingled with the scattered bones of a large *Camarasaurus*, No. 11393 C. M., and it might very well pertain to the same individual among whose skeletal parts it was found.

Although the large size and massiveness of this skull are in keeping with the general structure of the *Apatosaurus* skeleton, for the reasons discussed above it



was decided not to use the original skull to complete the skeleton but to substitute a replica, a temporary expedient to be used until such time as future discoveries shall disclose the true nature of the *Apatosaurus* cranium. It is the outline of this specimen that has been used to complete the restoration of the skeleton as shown in Pl. XXXIV.

In the first restoration<sup>7</sup> of the famous *Brontosaurus excelsus* skeleton made under the direction of Professor Marsh, the incomplete skull attributed to it is said by Lull<sup>8</sup> to have been found in Wyoming, near Como Bluffs, at a locality approximately four miles distant from the spot where the remainder of Marsh's type of *Brontosaurus excelsus* was obtained. In the emended restoration<sup>9</sup> of this skeleton, however, another skull was introduced slightly more complete than the first one used. This cranium corresponds in practically all details with a partial skull (No. 5730 U. S. N. M.) in the U. S. National Museum collection which came from the well known "Felsch Quarry" near Canyon City, Colorado, and of which Marsh had made a natural size drawing of the reconstructed skull. This drawing was never published except on the skeleton. This specimen was disassociated when found and thus there is no evidence as to its original affiliations. Furthermore, except for its very large size, I can find no characteristics that will definitely distinguish it from *Camarasaurus*.

After a review of all of the various skull parts that have been attributed to the genus *Apatosaurus*, it becomes quite evident that not in a single instance has there been such an association that we can definitely say this is a skull or a portion of a skull of *Apatosaurus*. At the present time we must therefore consider the skull of *Apatosaurus* as unknown.

#### VERTEBRAL COLUMN.

The complete vertebral column of *Apatosaurus* as shown by specimens in the Carnegie Museum, and first announced by the late Dr. William J. Holland,<sup>10</sup> has the following formula: Cervicals 15; dorsals 10; sacrals 5; caudals 82. The formula as stated may now be considered as positively determined for the genus *Apatosaurus*. The caudal series, however, may be found to vary in total number with the individual, even within a species.

Measurements made of the segments of the vertebral column in the mounted skeleton (No. 3018 C. M.), between perpendiculars, reveal the following interest-

<sup>7</sup>Marsh, O. C., Amer. Jour. Sci., vol. 26, 1883, Pl. I.

<sup>8</sup>Holland, W. J., Ann. Carnegie Museum, vol. IX, 1915, p. 275.

<sup>9</sup>Marsh, O. C., Dinosaurs of North America, Pl. XLII, 1896.

<sup>10</sup>Holland, W. J., Amer. Nat., Vol. LVII, 1923, pp. 477-480.



ing proportions: Cervical region, including the restored skull, 21 feet; dorsal, 8 feet, 7½ inches; sacral, 5 feet, 1 inch; and caudal, 36 feet, 9½ inches; a total length of 71 feet, 6 inches, between perpendiculars.

The backbone of *Apatosaurus* is characterized by the massiveness of the individual vertebræ; the absence of true pleurocoels in the caudals; and especially the stout heavy character of the cervical ribs.

As in other members of the Sauropoda, *Apatosaurus* has pleurocentral cavities in all of the presacrals, and paired spines in the postero-cervical and antero-dorsal regions.

The nomenclature used in the description of the various laminae and cavities is in the main that first proposed by Osborn.

#### CERVICAL VERTEBRÆ.

The fifteen cervical vertebræ preserved in the specimen were found in series. There was some distortion due to the compression to which they had been subjected, but this has been largely corrected during preparation. Cervicals thirteen, fourteen, and fifteen, however, were so badly crushed that it was thought best to replace them in the mounted skeleton by plaster restorations of these vertebræ. They are, however, sufficiently well preserved so that most of their important characteristics can be determined. In the present paper the illustrations of these bones were skilfully reconstructed by Mr. Prentice in order to make them more readily available for comparison with the other elements of the neck. Cervical ribs were present in all except C 1, C 2, C 3, C 14, and C 15. It is especially unfortunate that these posterior ribs are not well preserved as this transition from cervical to thoracic ribs is perhaps the least known portion of the Sauropod skeleton. The *Apatosaurus* cervicals are much stouter than those of *Barosaurus* and *Diplodocus* and differ from those of *Haplocanthosaurus* in having divided spines. In general they approach those of *Camarasaurus* more closely than any other Sauropodous dinosaur with which we are acquainted at this time.

*The Atlas.*—The atlas of specimen No. 3018 C. M. is completely preserved and is coössified with the axis, as shown in fig. 6. So close is the union of the centra of these two vertebræ that all trace of their junction has been obliterated except on the ventral surface, where the atlas intercentrum has a length of 54 mm. The odontoid was probably present but its recognition is no longer possible because of coalescence with the intercentrum. Due to this fact the intercentrum and odontoid when viewed from the front appear to be a solid block-like bone slightly wider than high with a moderately cupped face for articulation with the occipital condyle of the skull, see fig. 5. The neurapophysial processes are also fused with the intercentrum,

but their expanded ends probably contribute to the formation of the condylar cup as in other Sauropoda. Above this end the neurapophyses are constricted, but as they extend upward they rapidly expand into wide, comparatively thin processes that curve inward to cover and furnish protection to the spinal cord as it passes from the skull to the axis. The paired neuropophyses do not meet on the median line, but are separated a few millimeters at about the middle of their length.

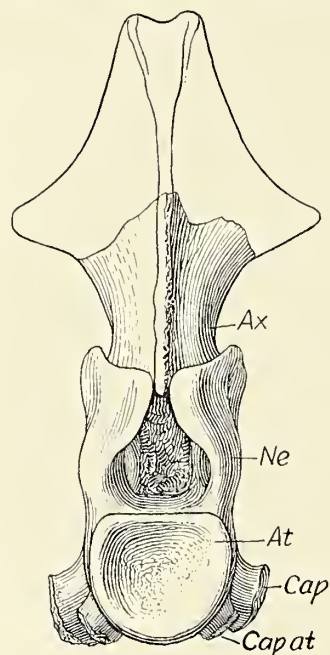


FIG. 5. Coalesced atlas and axis of *Apatosaurus louisae*. Type. No. 3018 C. M. Viewed diagonally from the front. *At.*, atlas; *Ax.*, axis; *Cap.*, capitular facet for articulation of cervical rib for axis; *Cap. at.*, capitular facet for cervical rib of atlas; *Ne.*, neuropophysis. One-fourth natural size.

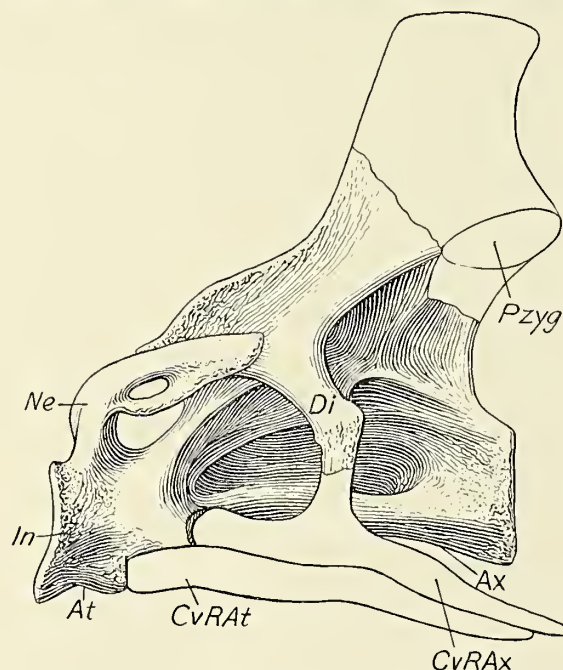


FIG. 6. Coalesced atlas and axis of *Apatosaurus louisae*. Type. No. 3018 C. M. Lateral view. *At.*, atlas; *Ax.*, axis; *Cv.R.At.*, cervical rib of atlas; *Cv.R.Ax.*, cervical rib of axis; *Di.*, diapophysis; *In.*, intercentrum; *Ne.*, neuropophyses; *Pzyg.*, postzygapophyses. One-fourth natural size.

Anterior and posterior to this point of near-median contact, their inner borders are strongly divergent as shown in fig. 5. The expanded process of the right neuropophyses is perforated by a sub-ovate opening, possibly the result of an old injury. The ventral surface of the intercentrum posteriorly is transversely hollowed out, on either side of which strong facets are developed for the articulation of the single-headed cervical rib.

#### MEASUREMENTS OF ATLAS

Width of atlas intercentrum.....	70 mm.
Height of atlas intercentrum.....	64 mm.
Length of atlas intercentrum on ventral surface.....	54 mm.

*The Axis.*—The axis is quite perfectly preserved except for the missing postzy-



gapophyses and top of the neural spine. The centrum is coalesced with the inter-centrum of the atlas, a condition not before observed in a member of the Sauropoda. The centrum is strongly opisthocoelus as is the case in all of the succeeding cervicals. There is a deep pleurocentral cavity on either side that extends forward into the base of the odontoid process. Viewed from below, the centrum is greatly constricted at mid-length, with expanded ends, more especially the anterior. The ventral surface of the anterior end is concave transversely being widened on either side by the development of heavy capitular processes for the articulation of the cervical ribs which are missing. The articular face of this process looks outward and strongly backward. Posterior to this process a deep longitudinal groove further lightens the side of the centrum, it disappears at about the middle length of the bone. The posterior blade of the horizontal lamina extends from the transverse process towards the posterior zygapophyses as in *Diplodocus*. A prominent transverse process springs from the middle of the sides of the arch. It is moderately broad and is directed downward, backward and outward and terminates in an enlarged articular end. The infradiapophysial lamina has an oblique position and gives support to the posteriorly directed transverse process in becoming a short laminar buttress connecting the process with the side of the neural arch and separating the infradiapophysial from the postdiapophysial cavity. The top of the neural arch is pinched together into a rounded median ridge that rises rapidly toward the spine, which is missing. Anteriorly this crest separates the two halves of the neurapophyses of the articulated atlas. The principal characters of the axis are well shown in fig. 6.

*Cervicals three to twelve.*—The cervical centra gradually increase in length from the first to the eleventh which is the longest of the series. In breadth and height there is a progressive increase from the first to the fifteenth. In form, the cervicals most nearly resemble those of *Camarasaurus* but have taller spinous processes and shorter and more robust cervical ribs.

The centra of the entire series are strongly opisthocoelus, the anterior balls being practically hemispherical in the forward half of the series and becoming transversely subelliptical in the posterior half. The walls of the centra appear to be of moderate thickness and the pleurocoelia are relatively small. The lateral walls of the centra slope upward and inward while the infrapostdiapophysial laminae project outward more or less horizontally on the hinder halves of the centra. The latter therefore roof over shallow asymmetrical depressions which Osborn and Mook call *external pleurocoelia*. From these depressions smaller but deeper cavities extend into the bodies of the centra. The number and shape of these cavities are variable, there are usually two but often three. The anterior one in



every case excavates the proximal portion of the parapophyses. Where there are three it appears that the posterior one is divided by a thin bar or accessory lamina. All of the cervical pleurocoels are relatively smaller than in other American Sauropod genera of equivalent age. Occasionally the anterior pleurocoele is divided. Inferiorly the centra are concave in both directions.

The neural arches of all of these vertebræ are comparatively low. Laterally they are crossed by anterior and posterior diapophysial lamina which separate off infraprezygapophysial, infradiapophysial, and infrapostzygapophysial cavities. The infraprezygapophysial cavity is situated above the anterior portion of the centrum and is bounded above by the horizontal lamina and below by the infraprediapophysial lamina. Posterior to C. 7, this cavity is bisected by an accessory lamina that extends upward and backward to unite with the horizontal lamina and cuts off a small accessory pocket that lies principally beneath the diapophyses. The infradiapophysial cavity is situated below the diapophyses, and is bounded in front and back by the anterior and posterior branches of the infradiapophysial laminae. The infrapostzygapophysial cavity lies above the posterior half of the centrum and is bounded above by the horizontal lamina and below by the posterior branch of the infradiapophysial lamina. They lie almost entirely behind the diapophyses.

The diapophyses, short and slender on the vertebræ of the anterior portion of the neck, progressively increase in length and in massiveness posteriorly. They project outward and downward in all of these vertebræ. The diapophyses in the anterior cervicals are situated rather far forward, but in the remaining cervicals this process is given off at about midlength, see B, Pl. XXIV. They are braced by the horizontal laminae above and below by the anterior and posterior branches of infradiapophysial laminae.

The parapophyses are strongly developed throughout the series. They are situated on the infero-lateral borders of the centra immediately posterior to the ball, and extend obliquely downward and outward, ending well below the ventral surface of the centrum. All are fully coössified with the capitulum of the cervical rib, an enlargement of the bone marking the point of their coalescence. Their superior surfaces merge into the walls of the centra and are excavated by a cavity, which may or may not be a subdivision of the pleurocoels of the centrum.

The prezygapophyses of all the vertebræ posterior to the axis are wide apart. Their articular surfaces look upward and inward. The prezygapophyses are braced from below by the infraprezygapophysial lamina, above by the slender supraprezygapophysial lamina; posteriorly by the horizontal lamina, and internally by the intraprezygapophysial lamina.

Viewed from the front, above the neural canal and below the intraprezygapophysial lamina are a pair of small cavities, separated on the median line by short, oblique laminae which unite on the median line and give support to the interprezygapophysial lamina.

The postzygapophyses are slightly higher and somewhat farther apart than the prezygapophyses. Their articular surfaces look downward and slightly outward. They are braced from above by the suprapostzygapophysial laminae, anteriorly by horizontal laminae, and inferiorly by infrapostzygapophysial laminae. Infraprezygapophysial laminae form the lower lateral boundaries of the neural canal, but commencing with C. 9 there are two small infraprezygapophysial cavities between the top of the canal and the intraprezygapophysial lamina. These cavities are separated by a short vertical lamina that braces the intraprezygapophysial lamina on the midline.

The spines as in *Camarasaurus* are situated over the posterior half of the centrum as far posteriorly as C. 7. From this point posteriorly the cervicals have the tops of the spines above the center of the centra. Unfortunately the type of *A. louisæ* lacks most of the spine tops, only those of cervicals eight, ten, and twelve being complete; thus the point of change from single to bifid spines cannot be determined in this specimen. In specimen No. 563, C. M., identified by Hatcher as pertaining to *Brontosaurus*, an identification with which I concur, there are nine cervical vertebrae preserved, three of which I regard as cervicals, three, four, and five. These show the spines to be single as far posteriorly as the fifth vertebra. Since C. 7 shows a well defined notch between the metapophyses, it seems to be a fair conclusion that C. 6 in *Apatosaurus* is the first vertebra to show a notch on the summit of the spine.

In *Camarasaurus supremus* Osborn and Mook<sup>11</sup> make the observation that, "In C. 5, the spine has a very slight median notch." In *C. lentus*,<sup>12</sup> however, the first notched spine is that of C. 7. From C. 6 to C. 9 inclusive, the spinal notch increases steadily in depth. From C. 9 to C. 15 inclusive, the spine is completely divided into two metapophyses.

Throughout, the spines are braced anteriorly by long supraprezygapophysial laminae, and posteriorly by shorter suprapostzygapophysial laminae. C. 2 to C. 5 are characterized by deep postspinal cavities below and behind the spines and between the postzygapophyses. Posterior to C. 5, they gradually reduce in size to C. 9, where the cavity has practically disappeared. C. 8, C. 10, and C. 12, show the

<sup>11</sup>Osborn and Mook, Mem. Amer. Mus. Nat. Hist., n.s., III, Pt. 3, 1921, p. 294.

<sup>12</sup>Gilmore, C. W., Mem. Carnegie Museum, X, No. 3, 1925, p. 369.



tops of the metapophyses to be bluntly truncated with a slight overhang of the anterior border. None show any transverse thickening of this end.

Beginning with C. 10 at the center between the bases of the metapophyses, there is a prominent rugose knob-like projection that extends backward and doubtless served as the attachment of one of the powerful intervertebral muscles, see 10, Pl. XXIV. This feature probably persists throughout the remainder of the cervical series, but due to the crushing of the posterior members this assumption cannot be certainly verified.

#### MEASUREMENTS OF CERVICALS

Vertebra No.	Greatest length of centrum		Greatest diameter cen- trum posterior end		Greatest breadth across transverse processes		Greatest height at center	
	C. M. No. 3018	C. M. No. 563	C. M. No. 3018	C. M. No. 563	C. M. No. 3018	C. M. No. 563	C. M. No. 3018	C. M. No. 563
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
1	45	...	...	...	...	...	125	...
2	190	...	85	...	150c	...	...	...
3	280	250	100	80	190c	185	...	315
4	370	300	100	125	355	280	...	360
5	...	342	...	134	...	315	...	380
6	440	...	150	...	430	...	...	...
7	450	415	190	170	485	425	...	...
8	485	415	225	205	545	480	560	...
9	510	445	230	215	635	520	...	560
10	530	475	250	250	750	640	...	...
11	550	...	240	...	675	...	825	...
12	490	...	265	...	770	...	815	...
13	480	...	...	...	684c	...	...	...

c = estimated.

#### DORSAL VERTEBRÆ.

The complete dorsal series of ten vertebræ are present in specimen No. 3018 C. M. All except the first articulated by their zygapophyses are shown in Fig. 3. The dorsals of *Apatosaurus* are distinguished by giving support to free ribs, instead of the coalesced or fixed ribs of the cervical region. There are no lumbar. The transition from cervical to dorsal is gradual except for the change in rib support, but more rapid than in *Diplodocus*. In the mounted skeleton only the centrum of D. 10 remains though in all probability all of this bone was originally present as shown in the quarry diagram, see fig. 3.

*The First Dorsal.*—The first dorsal in *Apatosaurus louisæ* is distinguished from all others by the small size of the pleuro-central cavity situated at mid-height and entirely on the posterior half of the centrum, and by the capitular facet developed



at mid-height on the centrum toward the anterior end. The centrum is strongly opisthocoelus and from the end is broadly ovate in outline. The paired neural spines or metapophyses, viewed laterally, are relatively narrow antero-posteriorly and there is no indication of a median spine such as Hatcher mentions on the first dorsal of *Diplodocus*. The neural arch is noticeably higher than in the posterior cervicals. The anterior and posterior zygapophyses are both somewhat more elevated than the diapophyses and are supported by the anterior and posterior blades of the horizontal laminae. The ends of both transverse processes are missing in this vertebra. They are supported from below by the short, rather slender inferior diapophysial lamina, which runs obliquely downward and forward to unite with the superior branch of the prezygapophysial lamina. An oblique, infradiapophysial lamina runs downward and backward from the diapophyses uniting with the neural arch near the top of the centrum. The pre- and supradiapophysial cavities are deep and well enclosed. The postdiapophysial cavity is shallow but clearly outlined. Viewed from the front, this vertebra appears low with greatly expanded transverse processes and zygapophyses. The neural spine is deeply bifurcated. Viewed from the front, the spines are broad at the base tapering rapidly to a slender extremity that from a side view has a slightly expanded truncate end, see Pl. XXV. The large anterior zygapophyses are joined by an intrazygapophysial lamina having the appearance of a sagging shelf. Inferiorly the zygapophyses are supported by robust infraprezygapophysial lamina. The infraprezygapophysial cavity is deep, and at the center divided by a heavy vertical lamina that arises immediately above the neural canal and extends upward to unite with the transverse lamina that joins the zygapophyses.

The suprapostzygapophysial lamina directed upward and outward form the posterior border of the spine. The infrapostzygapophysial laminae are pillar-like. The supra- and infrapostzygapophysial cavities are of moderate depth.

*Dorsals two and three.*—Compared with D. 1, the second and third dorsals may be distinguished at once by the successive elevation of the capitular facets, and a progressive increase in the size of the pleurocentral cavities. In D. 2, the capitular facet is on the side of the centrum at a level with its top; in D. 3, it occupies a position on the side of the arch about midway between the top of the centrum and the top of the prezygapophyses. In the type of *Apatosaurus excelsus* and in the Field Museum *Apatosaurus* specimen this condition is found on D. 4. Both centra are opisthocoelus, the ball much less prominently developed on D. 3. Both centra are broadly sub-ovate in outline. The diapophyses are stout, the ends being obliquely terminated by the tubercular facets for the ribs. They are supported from below by the greatly expanded infradiapophysial laminae, which reach their

strongest development in D. 2. From this vertebra posteriorly they gradually narrow dorso-ventrally. The diapophyses of both of these vertebræ extend outward and slightly downward below the horizontal. The spines or metapophyses as they are designated by Marsh are paired, and there is no indication of an incipient median spine as found by Hatcher<sup>13</sup> in *Diplodocus*. In D. 2, the notch between the metapophyses is wide and deep, but in D. 3, this notch is much narrowed, and somewhat shallower in depth. The articular surfaces of the postzygapophyses have assumed a more elevated position on D. 2, probably in anticipation of the development of the hyposphene-hypantrum method of articulation found for the first time on D. 3, see C, Pl. XXV. In D. 2, the postzygapophyses are supported by a pair of pillar-like infrapostzygapophysial laminae that arise from the arch, slightly above its junction with the centrum. In D. 3, however, these laminae are much reduced in size and, instead of being parallel as in the preceding vertebra, converge to meet where they join the hyposphene, and to which they give support. The infrahyposphenal cavity is bisected by a slender lamina that runs from the bottom of the hyposphene to the top of the neural canal. The articular surfaces of the pre- and postzygapophyses are wide apart but the postzygapophyses of D. 3 are closely joined, a feature that continues throughout the rest of the dorsal series. This wide spacing of the zygapophyses is a cervical feature that has been carried over into the dorsal segment. The anterior divided spines have practically the same laminar bracings as the single spines which succeed them. They are supported anteriorly by supraprezygapophysial laminae, posteriorly by suprapostzygapophysial laminae, and laterally by supradiapophysial laminae. These laminae extend obliquely upward and forward from the posterior sides of the diapophyses to the rugose summits of the spines. Thus they separate the anterior and posterior supradiapophysial cavities from each other. On D. 3, the supraprezygapophysial laminae pass obliquely downward from the top of the spines and join one another on the midline where they meet the transverse shelf that joins the two zygapophyses. At their junction a small incipient upward projection apparently marks the beginning of the prespinal lamina, which is well developed in the next dorsal posteriorly. At the center and on the posterior side of the lamina joining the two metapophyses of D. 2, is a rugosely developed projection that evidently marks the point of attachment of an important inter-vertebral ligament. In the next posterior dorsal this space is occupied by a short postspinal lamina. On the left side this lamina is buttressed by two short, oblique accessory laminae, an example of asymmetry noted in many of these vertebræ, as they have been in the vertebræ of other members of the Sauropoda.

<sup>13</sup>Hatcher, J. B., Mem. Carnegie Museum, vol. I, no. 1, 1901, p. 26.



*Dorsals four to ten.*—The centra of these vertebræ gradually shorten in a posterior direction. All are opisthocoelus, but the convexity is slight and confined entirely to the upper half of the centrum much as in *Diplodocus*, a feature that distinguishes these vertebræ from those of *Camarasaurus* which have well developed anterior balls throughout this portion of the vertebral column. Pleurocentral cavities are present in the entire dorsal series. Posterior to the third these are subequal in size and extend slightly into the base of the neural arch. The posterior ones are located nearer the anterior than the posterior borders. They are relatively smaller than in *Diplodocus* and *Barosaurus*. Neural arches are of moderate height. They consist, at the anterior borders principally, of the infraprezygapophysial laminae. These rise from the top of the centrum and are pillar-like in appearance. A single infradiapophysial lamina separates the infraprezygapophysial and infrapostzygapophysial cavities on the sides of the arches, in dorsals 4 to 8 inclusive. In D. 9, it is intersected by a short diagonal accessory branch rising from below on the side of the arch and forming a small infradiapophysial cavity. The infraprezygapophysial and infrapostzygapophysial cavities are bounded above by the horizontal laminae. The infradiapophysial laminae arise from the side of the arch well above the level of the centrum. The arches are much restricted fore and aft as well as transversely, never wider than the middle of the centrum. The parapophyses which bear the capitular rib facets are moderately well developed. On dorsals 4 to 8 inclusive, they are on a level with the prezygapophyses, but on D. 9, they drop to a point below the lower level of the prezygapophyses. They are supported principally by the infraprezygapophysial lamina. They comprise part of the thick mass of bone which is made up of the prezygapophyses and of the hypantra. The capitular facets face obliquely outward and downward, and slightly forward. These facets vary considerably in size, but become smaller posteriorly, see Pl. XXV. The pedicels become progressively longer in a posterior direction.

The diapophyses are long and extend outward at right angles to the perpendicular axes of the vertebræ, except in D. 9, which has an appreciable upward inflection above the horizontal. The diapophyses are supported from above by the supradiapophysial laminae, anteriorly and posteriorly by the horizontal laminae, and below by the infradiapophysial laminae. The tubercular facets face directly outward in all of the dorsals posterior to the fifth. In dorsals 4 and 5 they all look outward and downward.

The prezygapophyses are large throughout the dorsal series. In the anterior dorsals they are steeply inclined toward the median line, a condition that continues subequal as far back as D. 8. On the ninth, however, the prezygapophyses reach a nearly horizontal position. It is quite evident that the missing prezygapo-



physes of the tenth dorsal would be horizontal, as indicated by the horizontal position of the postzygapophyses of D. 9, see Pl. XXV.

The postzygapophyses are equal in size and in inclination to the prezygapophyses described above. They are supported from below, where they join on the median line by the bases of the hyposphene.

The hyposphene-hypantrum articulation is present on all of the dorsal vertebræ beginning with the third. The hyposphenes extend downward from the point on the midline where the postzygapophyses join.

Immediately below the zygapophyses the hyposphenes are narrow transversely, but below this narrow part they rapidly expand into a diamond-shaped process that is braced from below by a single vertical lamina that fades out on the median posterior face of the arch about half way between the hyposphene and the neural canal. Each hyposphene has two articular faces on its exterior and superior surfaces. These faces are continuous with the postzygapophyses. They look outward on the constricted portion, and upward and outward on the expanded part. The hyposphene reaches its strongest development on D. 4, and progressively decreases in size posteriorly. Dorsal 4 is the first to show a hypantrum. Each hypantrum consists of a pair of articular surfaces located below the prezygapophyses. The hypantral surfaces are continuous with the postzygapophyses and face obliquely downward and inward, nearly at right angles to the prezygapophyses. When articulated the hyposphene fits in between and under the hypantra thus giving strong support to the zygapophyses in locking the vertebræ together. This form of articulation of the vertebræ makes a very rigid backbone, as there is little chance for movement except in an antero-posterior direction.

The spines of the dorsal vertebræ gradually increase in height from front to back. In D. 4, the spine is wide, transversely and moderately notched; in D. 5, the spine is much narrowed with a notch slightly less deep. In D. 6, the notch is shallow, and D. 7 shows no indication of a notch. In *Diplodocus* this notch is present on the spine of D. 9, and *Camarasaurus* shows only a slight indication of it on the spine of D. 7. The spines are elongate as a whole in the posterior half of the dorsal series. Those behind D. 6 have the spines forming more than one half the total height. The laminae bracings consist of supraprezygapophysial laminae in front and suprapostzygapophysial laminae behind. The former are supported laterally by short supradiapophysial laminae.

These laminae as far posterior as D. 5, are distinct and continue upward to the top of the spine, but on D. 6, they merge with the suprapostzygapophysial to form a single wide lamina when viewed from the side. This lamina narrows antero-posteriorly on the succeeding dorsals except for the expanded top as far posterior

as D. 8. On the ninth the supradiapophysial branch disappears. On the middle line of both front and back sides of the spine are pre- and postspinal laminæ, the posterior usually being more robust than the anterior. These run the full length of the spine with a tendency to bifurcate at the bottom where they unite with the pre- and postzygapophyses. These laminæ separate subequal elongate depressions on either side, especially on the upper half of the spines. None of these laminæ extend to the summit but all merge into the rugose head.

All of the tenth dorsal is missing above the centrum, and for that reason has not been illustrated with the other dorsal vertebræ on Pl. XXV.

Among the unpublished plates of *A. (Brontosaurus) excelsus* (Marsh) prepared for Professor O. C. Marsh by the U. S. Geological Survey are excellent illustrations of the third, fourth, fifth, and eighth dorsal vertebræ. These have been critically compared with the corresponding vertebræ of *Apatosaurus louisæ* and some interesting differences of structure are found, the most important being the fact that D. 4 in *A. excelsus* in its structural features is equivalent to D. 3 in *A. louisæ*. It is the first vertebra to develop a hyposphene; the capitular facet is on the side of the arch about midway between the centrum and the prezygapophyses, and the centrum has a well developed ball. Since practically these same conditions occur in the Field Museum *Apatosaurus* specimen with the exception of a ball on the centrum, it may indicate that in *A. excelsus* we have an advanced structural specialization or cervicalization of the anterior dorsals not found in *A. louisæ*.

#### COMPARATIVE MEASUREMENTS OF DORSAL VERTEBRÆ

Verte- bra No.	Greatest length of Centrum			Greatest diameter cen- trum posterior end			Greatest height of vertebra above middle of inferior border		
	C. M. No. 3018	C. M. No. 563	F. M. No. 7163	C. M. No. 3018	C. M. No. 563	F. M. No. 7163	C. M. No. 3018	C. M. No. 563	F. M. No. 7163
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
1	310	345	370	355	335	400	845	...	490
2	315	285	360	355	365	410	850	855	530
3	310	280	330	350	330	410	885	869	580
4	260	213	290	315	345	400	995	915	720
5	260	235	290	335	315	410	1060	...	880
6	270	260	280	335	305	400	1060	...	1060
7	260	235	260	335	335	410	1275c	...	1200
8	275	225	300	350	340	410	1340c	...	1290
9	255	230	250	315	355	410	1350	...	1310
10	240	...	250	365	...	400	...	...	1340

c = estimated.

#### SACRAL VERTEBRÆ

There are five coössified vertebræ in the sacrum of *Apatosaurus louisæ*, No. 3018 C. M. All of these vertebræ function as sacrals, although in this specimen,



as it has been shown in practically all adult members of the Sauropoda, the primary sacrum consists of the three median vertebræ. These are augmented by a vertebra in front, a sacrodorsal, and by a vertebra at the back, a sacrocaudal. This feature of the Sauropod skeleton has been thoroughly discussed by Riggs,<sup>14</sup> Hatcher,<sup>15</sup> and Osborn and Mook<sup>16</sup> and there appears no necessity of discussing this question at this time.

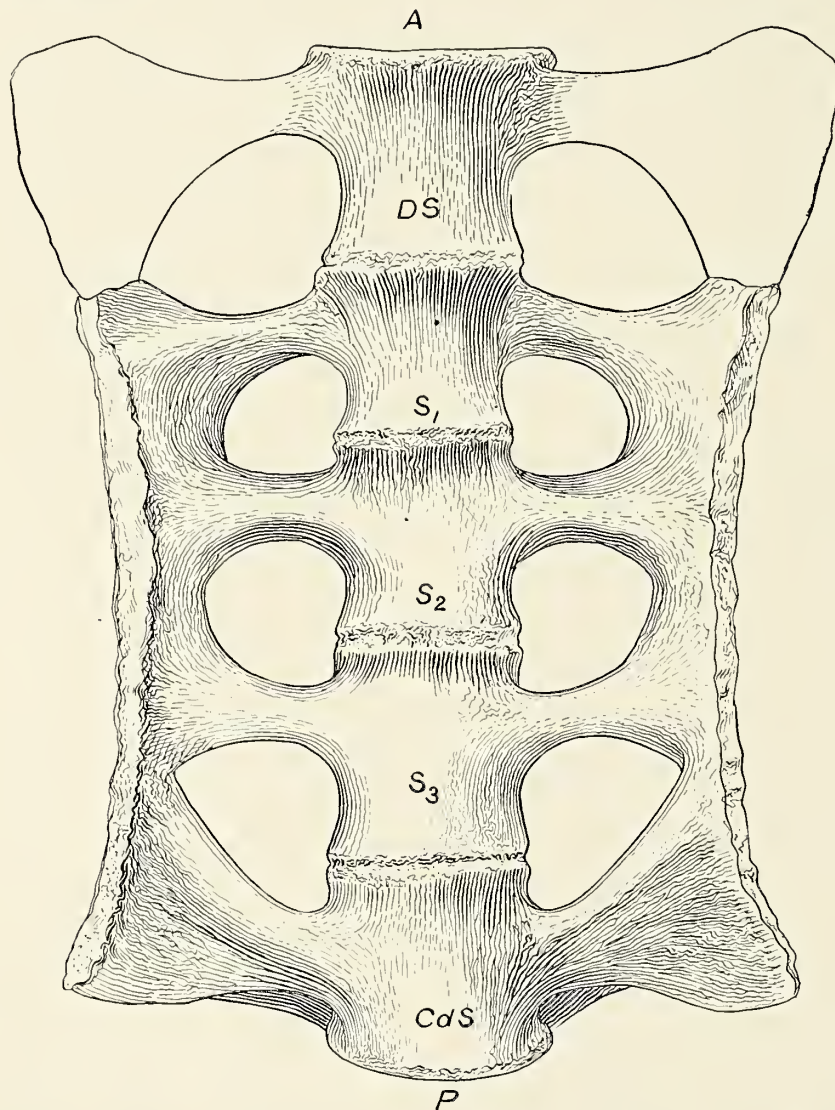


FIG. 7. Sacral vertebræ of *Apatosaurus louisæ*. Type. No. 3018 C. M. Ventral view. A., anterior end; Cd-S., caudo-sacral; D-S., dorso-sacral; P., Posterior end; S<sub>1</sub>, S<sub>2</sub>, S<sub>3</sub>, primary sacrals, one, two, and three. One-tenth natural size.

<sup>14</sup>Riggs, E. S., Field Columbian Museum, Pub. S2, II, Geol. Ser., No. 4, 1903, pp. 180-186.

<sup>15</sup>Hatcher, J. B., Memoirs Carnegie Museum, I, 1901, No. 1, pp. 30-34; Ibid. II, 1903, No. 1, pp. 14-18.

<sup>16</sup>Osborn, H. F., and Mook, C. C., Memoirs American Museum Natural History, III, 1921, Pt. III, pp. 309-316.



In the restored condition of the present sacrum the ventral side is practically all that is visible for examination. The spinous processes and diapophyses are all restored. That these parts were originally present appears to be indicated by the fact they were sketched in on the quarry map, and in all probability have since been destroyed through the vicissitudes of collecting and preparation.

A ventral view of the coössified sacral centra is shown in fig. 7. These vertebræ have a combined length of about 1325 mm., divided between the five elements as follows: D-S, 275 mm.; S<sub>1</sub>, 225 mm.; S<sub>2</sub>, 260 mm.; S<sub>3</sub>, 295 mm.; Cd-S, 275 mm. The inferior surfaces of the centra are broadly rounded. In this view the sides of the centra are much less constricted than in either the dorsals which precede, or the caudals that succeed them. The sacral ribs are all fully coalesced with the centra, and except in the caudosacral, which unites centrally, the others arise from the antero-lateral surfaces of the centra. In *Apatosaurus excelsus*<sup>17</sup> as shown in the type, and in the Field Museum specimen<sup>18</sup> the first two ribs arise from the mid-lateral surfaces on the centra. The outer ends of the sacral ribs are much expanded and completely fused with one another into a horizontal plate or bar that gives support to the ilium on either side. They enclose four sacral cavities on each side. The shafts of these ribs are more slender than in *A. excelsus* and their proximal ends are much less expanded than in that species, excepting S<sub>5</sub>, all of the centra articulate with the ribs on their anterior halves; whereas in *A. excelsus* they attach the full length of the centra.

Viewed from the side, see fig. 19, the articular faces of the first and last sacral are not parallel but lean toward one another at the top, a condition found in other Sauropod sacra. This feature, when the vertebræ are properly articulated, causes the column to arch slightly upward both forward and back of the sacrum and brings about a lizard-like posture to this part of the vertebral column. Unfortunately in most of the mounted Sauropod skeletons, the articulation of these bones has been modified, as in the present instance, by preconceived ideas and the true curves of the column at these points have been lost.

#### CAUDAL VERTEBRÆ.

In addition to the articulated caudal series of 64 vertebræ pertaining to the type of *Apatosaurus louisæ*, No. 3018 C. M., there was available for this study two other specimens of *Apatosaurus* in the Carnegie Museum collection having good series of caudal vertebræ. The first, No. 3378 C. M., is a complete, articulated vertebral column, of which 82 vertebræ constitute the caudal region. This is the

<sup>17</sup>Marsh, O. C., *Dinosaurs of North America*, Pl. XXIII, 1896.

<sup>18</sup>Riggs, E. S., *Field Columbian Museum*, Pub. 82, Geol. Ser. II, No. 4, 1904, Pt. I, p. 179.

only complete, articulated vertebral column of *Apatosaurus* known at this time. The specimen is a considerably smaller individual than the type, but comes from the same quarry, see Pl. XXIII, Field No. 160. The second specimen, No. 563 C. M., from Sheep Creek, Albany County, Wyoming, is also slightly smaller than the type of *Apatosaurus louisæ*. With this disarticulated skeleton there were 18 caudal vertebræ representing practically all parts of the tail except the whip-lash portion. This specimen was identified by Hatcher<sup>19</sup> as pertaining to *Brontosaurus*. A study of all three of these specimens has made it possible to determine nearly the complete structure of the tail. The outstanding feature of the *Apatosaurus* tail is its great length, especially the attenuated whip-lash portion.

The caudal series of specimen No. 3018 C. M. consists of 64 vertebræ, of which the anterior 26 were articulated by their zygapophyses with the sacrum. The remaining vertebræ were found in such relationship to the articulated parts as to leave no doubt that all pertain to this one individual. Their relative positions as found in the quarry are clearly shown in fig. 3. In the mounted skeleton these caudal vertebræ have been articulated as a continuous series and no reason has been found for not so regarding them. Their regularly graduated continuity (when allowance is made for slight distortion) appears to indicate the correctness of their arrangement.

This specimen was the first one found giving absolute information that *Apatosaurus* had a long whip-like extension of the tail such as had been previously discovered in the genus *Diplodocus*.

In completing the tail of the mounted skeleton, nine additional artificial elements were added to the tip making a total of 73 vertebræ. That the complete series is in excess of that number is now clearly shown by specimen No. 3378 C. M., see Pl. XXVIII, of which the complete series formed a part of an articulated vertebral column that extended from the atlas to the very tip of the tail. There are 82 caudal vertebræ in this series, as now numbered, although an elongated element near the tip may represent a coalesced pair in which event the total would be 83. In all probability this number varies with the individual even of the same species. There must have been great liability of loss from the tip of such a slender appendage, and the uniformity in size of these terminal rod-like caudals is such that any loss would be difficult of detection.

In 1915, Dr. Holland<sup>20</sup> briefly mentioned this specimen, No. 3378 C. M., of which he published an illustration of the distal portion of the series (Nos. 34 to 82) but at that time made no mention of the genus to which it pertained. I have

<sup>19</sup>Hatcher, J. B., Annals Carnegie Museum, vol. I, Art. 13, 1902, p. 356.

<sup>20</sup>Holland, W. J., Annals Carnegie Museum, vol. IX, 1915, p. 27, Pl. LIX.



compared this series with the corresponding vertebræ of the mounted skeleton and such close agreement is found as to leave no doubt of their being congeneric. Although the complete tail represents a considerably smaller animal than No. 3018 C. M., the heavy solid nature of the centra, the disappearance of the transverse processes on the fifteenth caudal, and correspondence of the points of change in the form of centra and spinous processes show the two specimens to be in close accord.

The anterior caudal vertebræ, as far posteriorly as the seventh, may be described as procœlus. The anterior faces of all these vertebræ are concave; the posterior face slightly concave on the upper fourth, but with a pronounced ball on the lower three-fourths of this end in the first caudal, as shown in Pl. XXVI. This convexity grows progressively smaller in a posterior direction, disappearing entirely on the seventh caudal vertebra. Riggs<sup>21</sup> notes a similar change in the anterior caudals of the Field Museum *Apatosaurus*. It thus grades into an uncertain amphicœlous type of centrum, beginning with the seventh, that persists to the thirty-fourth caudal. On the thirty-fourth a ball again appears on the posterior end. On the thirty-fifth there is a ball on both ends, and this type of articulation persists throughout the slender "whip-lash" extremity of the tail, a style of articulation that permits of the greatest mobility in all directions.

Viewed from the end the centra of the first six caudal vertebræ are considerably higher than wide, a proportion that distinguishes these vertebræ of *A. louisæ* from the homologous elements of *A. (Brontosaurus) excelsus* which are subequal in these two diameters. Likewise, as shown by the type of *A. excelsus*, and the two referred specimens, the Field Museum *Apatosaurus* and No. 563 C. M., the procœlus type of centrum begins with C. 2, instead of C. 1, as in *A. louisæ*.

The centra are relatively short antero-posteriorly as compared with *Diplodocus*, and all are constricted medially. With some slight exceptions they grow progressively shorter from first to last. Likewise, the centra become successively smaller in all other diameters as far posteriorly as the fortieth caudal, but posterior to this point the centra, except in length are rod-like and continue with slight diminution to the very tip.

The neural arch is low and massive throughout. In the type specimen, No. 3018 C. M., the arch persists as far back as C. 32, see Pl. XXVII. In specimen No. 3378 C. M., the last complete arch is found on C. 35, see Pl. XXVIII. The arches are simple, not divided by laminæ as in the cervicals and dorsals. The first fourteen caudal vertebræ posterior to the sacrum bear transverse processes, see Pl. XXVI. A similar number are present in No. 3378 C. M., whereas in the Field

<sup>21</sup>Riggs, E. S., Field Columbian Museum, Geol. Ser. II, No. 4, 1903, p. 189.



Museum specimen, Riggs recognized only twelve. The resoration of this specimen made under his direction shows more. He calls attention<sup>22</sup> to the fact that the Yale specimen, the type of *Apatosaurus excelsus* has only twelve caudals bearing transverse processes, and the American Museum specimen eleven. Since the caudal vertebrae of the latter were not found articulated, the number cited may or may not be correct. In any event the agreement among these specimens is fairly close, for the place of disappearance of such a vestigial process could hardly be expected to be constant. The transverse processes on the first caudal are largely missing, but enough remain, see Pl. XXVI, to show the great dorso-ventral expanse, and also to indicate that these wing-like processes were not perforated by foramina-like openings as in the first caudal of the type *A. (Brontosaurus) excelsus* Marsh.

These expanded wing-like transverse processes continue backward to C. 6, where they are reduced to a roughened vertical ridge. These processes spring from the side of the arch and centrum, projecting outward at right angles to the main body of the vertebrae. The upper horizontal borders are on a level with the zygapophyses, and the outer borders of the first six slope obliquely downward to about mid-depth of the centrum. Where the superior and outer borders intersect, prominent shoulders are developed which persist as far posteriorly as C. 5. Posterior to the fifth caudal, the top of the oblique outer border merges directly into the side of the neural arch. This oblique border is rugosely roughened and overhangs the vertical laminae on both the anterior and posterior sides. On the posterior side, the surface of the transverse process is fairly smooth, but on the anterior face each process is pocketed by a pair of shallow depressions placed one above the other. On C. 3, the lower depression exists as a rounded, well defined foramina-like opening that gives entrance to the interior of the process. In *A. louisæ* none of the transverse processes is entirely perforated as found in the anterior caudals of at least two specimens of *A. excelsus*. Holland<sup>23</sup> cited this difference as one of the specific characters for distinguishing the two species. In all probability this feature will vary with the individual. Posterior to the sixth caudal vertebra the transverse processes or caudal ribs are simple in character, gradually decreasing in size posteriorly and finally disappearing entirely after the fourteenth caudal vertebra.

The prezygapophyses are moderately well developed but small in comparison with the size of the vertebrae. They decrease regularly in size in a posterior direction and persist as far posteriorly as the thirty-second caudal and were functional as far back as the twenty-fifth vertebra. In specimen No. 3378 C. M., nonfunc-

<sup>22</sup>Riggs, E. S., *idem*, p. 188.

<sup>23</sup>Holland, W. J., *Annals Carnegie Museum*, X, Art. 10, 1915, p. 2.

tional prezygapophyses are present on the thirty-fifth, and in this series they also articulate as far back as the twenty-eighth.

The prezygapophyses of the anterior seven are supported from below by heavy infraprezygapophysial laminae that rise from the centrum. The articular surfaces look strongly upward and inward. They extend forward and overhang the end of the centra. Superiorly they are braced by supraprezygapophysial laminae; these laminae disappear at some point between the third and the eighth vertebrae. Unlike the anterior caudals in *Camarasaurus* and *Haplacanthosaurus*, additional support is given the prezygapophyses in caudals one, two, three, and four, by a short horizontal lamina running from the top of the transverse process. This lamina, however, is not present on the posterior side.

The postzygapophyses are situated at the bases and somewhat beneath the spines. Functional postzygapophyses are found as far back as the twenty-fifth vertebra, and vestigial articulations are to be observed on the thirty-second. The articular surfaces look strongly downward and outward. In the four anterior caudal vertebrae the postzygapophyses are supported at their junction by a median vertical plate that arises from the arch above the neural canal. This plate has been designated the "*intraspinous lamina*" by Osborn and Mook<sup>24</sup> but I am of the opinion that it represents a vestige of a hyposphenal articulation. This idea is given support, especially by the transverse expansion of this plate as shown in B, Pl. XXVI. From above, the postzygapophyses are braced by the suprapostzygapophysial laminae.

The spinous processes are partially or wholly missing as far posteriorly as the eighth caudal in specimen No. 3018 C. M.

The first, second, and third caudals lack their upper extremities. In the illustrations, see Pl. XXVI, these missing parts have been drawn in outline from the vertebrae as restored in the mounted skeleton. When compared with the complete first caudal of *A. excelsus*, No. 563 C. M., an individual shown, by the measurements of the limb and other bones, to be of approximately the same size, it could appear that these spines as restored are somewhat too long. On the other hand the spines throughout the anterior caudal and dorsal region are more attenuated than in *A. excelsus*.

The spines of the first three caudals are composed primarily of prezygapophysial, postzygapophysial, heavy prespinal, and less well developed postspinal laminae. These laminae largely disappear as separate structures in the vicinity of the twelfth caudal. In the anterior caudal region, the summits are broader than their bases. From the region of caudal thirteen, posteriorly, there is little transverse expansion of the upper termination and the spines are flat and plate-like.

<sup>24</sup>Osborn, H. F. and Mook, C. C., Memoir Amer. Mus. Nat. Hist., N.S., III, Pt. III, 1921, p. 320.



The spines of the anterior vertebræ are relatively narrow, antero-posteriorly, but between the thirteenth and twenty-second they gradually widen. A vestigial spine is present on the thirty-second. The progressive changes in the form of the spines from front to back in *Apatosaurus* are best shown in specimen No. 3078 C. M., see Pl. XXVIII. I find no evidence of the emargination of the tops of the spines of the anterior vertebræ as in *Diplodocus*.

An interesting feature of the tail in this specimen is the coössification of caudals twenty-two and twenty-three, see fig. 8. Their condition is probably attributable to traumatic causes since there is an excess of extraneous bony matter extending over the joint comparable in a way to the diseased Sauropod caudals described and illustrated by Moodie.<sup>25</sup> In *Diplodocus* there are no less than three specimens known having coössification of the caudal vertebræ in practically the same region of the tail. Hatcher<sup>26</sup> was the first to suggest that it occurred at the point where the tail first touched the ground and for that reason was more susceptible to injury. With the dorsal elevation of the tail as it leaves the sacrum, a condition now known to prevail in most of the Sauropoda, it no longer touches the ground in this region but posterior to it, thus this explanation no longer obtains. The possible suggestion has been made that in rearing up on the hind legs this portion of the tail would be brought into use as a support and that injury might at times result from the strain to which it was subjected.



FIG. 8. Coössified caudal vertebræ (22d and 23d) of *Apatosaurus louisæ*. Type. No. 3018 C. M. Viewed from left side. About one-fifth natural size.

Moodie<sup>27</sup> has the following to say regarding these vertebræ: "A badly infected lesion, showing on the surface several large necrotic sinuses, indicates an injury

<sup>25</sup>Moodie, R. L., Amer. Jour. Sci., vol. 41, pp. 530-531, fig. 1, 1916.

<sup>26</sup>Hatcher, J. B., Memoirs Carnegie Museum, vol. I, no. 1, 1901, p. 37.

<sup>27</sup>Moodie, R. L., Paleopathology, 1923, p. 165.



to the tail of a large dinosaur *Apatosaurus louisæ*, in the Carnegie Museum. It may be an example of spondylitis deformans, though other lesions of this nature seen in the tails of dinosaurs do not possess necrotic sinuses. It may be an osteomyelites or an incipient hemangioma. A *Diplodocus* skeleton in the same museum exhibits two lesions on the tail, around which have developed a pathology similar to spondylitis deformans. The injuries in both dinosaurs are near the point where the tail reaches the ground, and it may well be that trauma is the cause of them all."

Specimen No. 3378 C. M. also shows the beginning of a coössification of the twenty-second and twenty-third caudal vertebræ, by the uniting of the spinous processes, see Pl. XXVIII.

#### CHEVRONS.

There were only three chevrons preserved with specimen No. 3018 C. M. These, however, were found articulated and thus give positive evidence that the first chevron articulates with the first caudal vertebra. Riggs found one below the first caudal in the *Apatosaurus* skeleton in the Field Museum (Field Columbian Mus., Pub. 82, vol. 2, 1903, p. 191) and on the evidence of this specimen it is now certain that all of the anterior caudals were chevron bearing. All three of the chevrons have the hæmal canal entirely closed in by a bridge of bone. The first is shorter than the second chevron, but not as short as the one figured by Riggs. The missing chevron bones on the mounted skeleton have been restored after those of the Field Museum specimen but those were found disarticulated so that their positions cannot be considered as precisely determined. The distal end of the third chevron in the present specimen is restored.

Chevron facets appear to be present as far posteriorly as the thirty-third caudal. In specimen No. 3378 C. M., there is a portion of a chevron attached to the thirtieth caudal, see Pl. XXVIII. On the restoration, Pl. XXXIV, chevrons have been restored after the above evidence.

#### MEASUREMENTS.

Greatest length of first chevron.....	360 mm.
Greatest length of second chevron.....	405 mm.

#### RIBS

All of the presacral vertebræ in *Apatosaurus* are rib bearing. The cervical ribs are stout and seldom exceed the centra in length.

*Cervical ribs.*—All of the cervical ribs that are present are fully ankylosed with their respective vertebræ. They are entirely missing from the atlas, axis, C. 3, C. 14, and C. 15. The tubercular processes extend outward and downward from

## COMPARATIVE MEASUREMENTS OF CAUDAL VERTEBRÆ

No.	Greatest length of centrum				Transverse diameter posterior end				Greatest height over all			
	<i>A. louisæ</i> No. 3018 C. M.	<i>A. excelsus</i> No. 7163 Field Mus.	<i>A. excelsus</i> No. 563 C. M.	<i>A. sp.</i> No. 3378 C. M.	<i>A. louisæ</i> No. 3018 C. M.	<i>A. excelsus</i> No. 7163 F. M.	<i>A. excelsus</i> No. 563 C. M.	<i>A. sp.</i> No. 3378 C. M.	<i>A. louisæ</i> No. 3018 C. M.	<i>A. excelsus</i> No. 7163 F. M.	<i>A. excelsus</i> No. 563 C. M.	<i>A. sp.</i> No. 3378 C. M.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
1	240	192	150	...	300	390	325	...	1250e	1130	1005	...
2	205	220	155	...	290	380	305	...	1120e	1010	...	...
3	215	230	160	140	280	360	295	...	1020e	920	735	...
4	190	230	160	145	280	350	270	...	920e	870	...	...
5	190	220	160	145	285	330	265	...	830e	760	...	...
6	175	210	150	...	250	310	255	...	765e	680	595	...
7	190	200	150	140	260	300	225	...	675e	630	510	...
8	185	200	150	...	245	290	215	...	625	530	495	...
9	185	200	155	155	240	290	195	165	575	530	420	...
10	190	200	...	149	240	290	...	...	530	500	...	420
11	190	190	155	150	235	280	225	165	500	520	...	368
12	200	200	...	147	220	260	...	160	475e	470	...	355
13	195	200	175	160	215	250	190	165	470	470	380	...
14	200	210	...	160	190	220	...	164	...	420	...	...
15	200	220	...	167	190	220	...	161	...	410	...	...
16	...	220	205	170	...	210	235	155	...	380	365	...
17	205	220	190	172	170	210	195	137	...	360	355	...
18	200	330	...	178	170	200	...	...	...	330	...	...
19	200	310	...	181	185	210	...	130e	...	310	...	210
20	225	300	...	183	165	190	...	112	...	300	...	...
21	210	280	...	161	150	180	...	110	...	280	245	210
22	405	270	...	174	...	170	...	...	...	270	...	210
23	...	250	190	170	131	170	111	109	...	250	...	200
24	195	...	...	177	145	...	...	107	...	...	...	190
25	205	...	185	168	125	...	105	90e	...	...	220	185
26	188	...	175	165	125	...	110	...	...	...	...	175
27	190	...	...	165	105	...	...	80e	...	...	...	170
28	200	...	...	150	100	...	...	80	...	...	...	155
29	180	...	...	145	86	...	...	70e	...	...	...	140
30	175	...	160	140	83	...	80	67	...	...	...	130
31	170	...	160	135e	76	...	65	60	...	...	...	...
32	163	...	...	139	69	...	...	50	...	...	...	110
33	160	...	...	132	55	...	...	40	...	...	...	85
34	153	...	...	140	48	...	...	30	...	...	...	77
35	155	...	...	122	45	...	...	30	...	...	...	50
36	152	...	...	127	44	...	...	27	...	...	...	...
37	151	...	...	110	46	...	...	20	...	...	...	50
38	145	...	...	...	38	...	...	...	...	...	...	...

[illegible]

$e = \text{estimated.}$



the diapophyses and in this way add considerably to the width of the neck. The capitular process is usually the stouter one of the two and it extends inward and upward to join the capitular facet of the vertebra. The shafts of the ribs extend backward parallel with the centra but well below their ventral borders. They taper rapidly to an obtuse end that seldom reaches a point beyond the posterior end of the centrum. In none of the cervical ribs of this specimen is there a forwardly projecting end as in *Diplodocus*, or as in many of the ribs of No. 563 C. M., see Pl. XXXI. There is, however, a heavy blunt projection that extends downward and slightly backward. On the inner side the shaft is hollowed out.

The stoutness of the cervical ribs of *Apatosaurus* furnish one of the outstanding characters of the genus. Their stoutness of structure at once distinguishes them from the slender cervical ribs of *Diplodocus*, and from the long attenuated ribs of *Camarasaurus* and *Barosaurus*.

*Thoracic Ribs.*—There are twenty thoracic ribs in *Apatosaurus*, and eighteen of these are preserved with the present skeleton. The tenth pair is missing. None of the ribs was found articulated, see fig. 3, but all are in a good state of preservation. Those of the left side correspond very closely with those of the right which are illustrated in Pl. XXIX.

The first rib differs from all of the others in having a nearly straight shaft, and in having the peduncle bearing the capitulum nearly at right angles to the main axis of the bone. From the union of the capitulum with the tuberculum the shaft diminishes very gradually to a point near the distal end. The tuberculum and capitulum are subequal in size and supported on peduncles of subequal length. The distal end is truncated. The second, third, and fourth are the stoutest of the series. The ribs increase in length from the first to the sixth which is the longest. From the sixth posteriorly they rapidly shorten, the ninth being only a little more than one half the length of the sixth. The second rib presents a broad and rather flat external surface. Near the distal end, the bone is slightly expanded, with a noticeable backward inclination. The anterior surface of the shaft below the head is perforated by a large foramen which leads to an internal cavity.

The tuberculum and capitulum, far apart in the first rib, gradually approach one another posteriorly. Beginning with the fourth, when placed in a vertical position, the capitulum projects high above the tuberculum but in a posterior direction this relationship is progressively altered until in the ninth they are nearly on the same level. No trace was found of either of the tenth pair. In the Field Museum specimen<sup>28</sup> the right one of the tenth pair was coössified with the vertebra, while the distal end abutted the crest of the ilium.

<sup>28</sup>Riggs, E. S., *idem.*, p. 177.

From this evidence it would appear that the restored rib in the mounted skeleton had been made too long. The principal features of the ribs are clearly indicated in Pls. XXIX and XXX.

## COMPARATIVE MEASUREMENTS OF RIBS

Rib No.	Length		Breadth across head and tubercle		Breadth at middle of shaft	
	C. M. No. 3018	F. M. No. 7163	C. M. No. 3018	F. M. No. 7163	C. M. No. 3018	F. M. No. 7163
	mm.	mm.	mm.	mm.	mm.	mm.
1	1475	...	475	430	90	80
2	1615	...	450	510	100	95
3	1980	...	375	500	90	130
4	2025	...	350	440	105	130
5	2060	2130	340	405	95	125
6	2075	2070	310	420	90	85
7	1820	1850	290	360	90	90
8	1665	1700	270	310	85	85
9	1140	1260	300	250	60	80
10	...	620	...	240	...	60

## PECTORAL GIRDLE.

The pectoral girdle is represented by the coalesced scapula and coracoid of both sides, but no trace was found of the sternal plates.

*Scapula*.—Both scapulæ and coalesced coracoids are present with this specimen, and both are in excellent preservation. Viewed from the side the outline of the scapula of *Apatosaurus louisæ* is intermediate in form between that of the type of *A. (Brontosaurus) excelsus* and the type of *Apatosaurus ajax*, as is clearly shown in fig. 10. In the straightness of the posterior border, and the slight expansion of the upper end, it is nearer to the last named species than to *A. excelsus*.

The proximal end of the scapula is broadly expanded, this breadth being about one-half the total length of the bone. From end to end it is regularly curved as in all members of the Sauropoda, see C, fig. 9.

On the external side, between the coraco-scapula suture and the spine or ridge that extends diagonally across the expanded proximal end, the surface of the bone is concave forming an area of considerable extent for muscular attachment. On the upper side of this ridge the surface slopes off gradual to the border, there being hardly any evidence of a superior fossa so prominently indicated in the *Camarasaurus* scapulæ, and to a slightly less degree in the scapula of *A. excelsus*. The superior border is somewhat thickened transversely, with a slight expansion of this



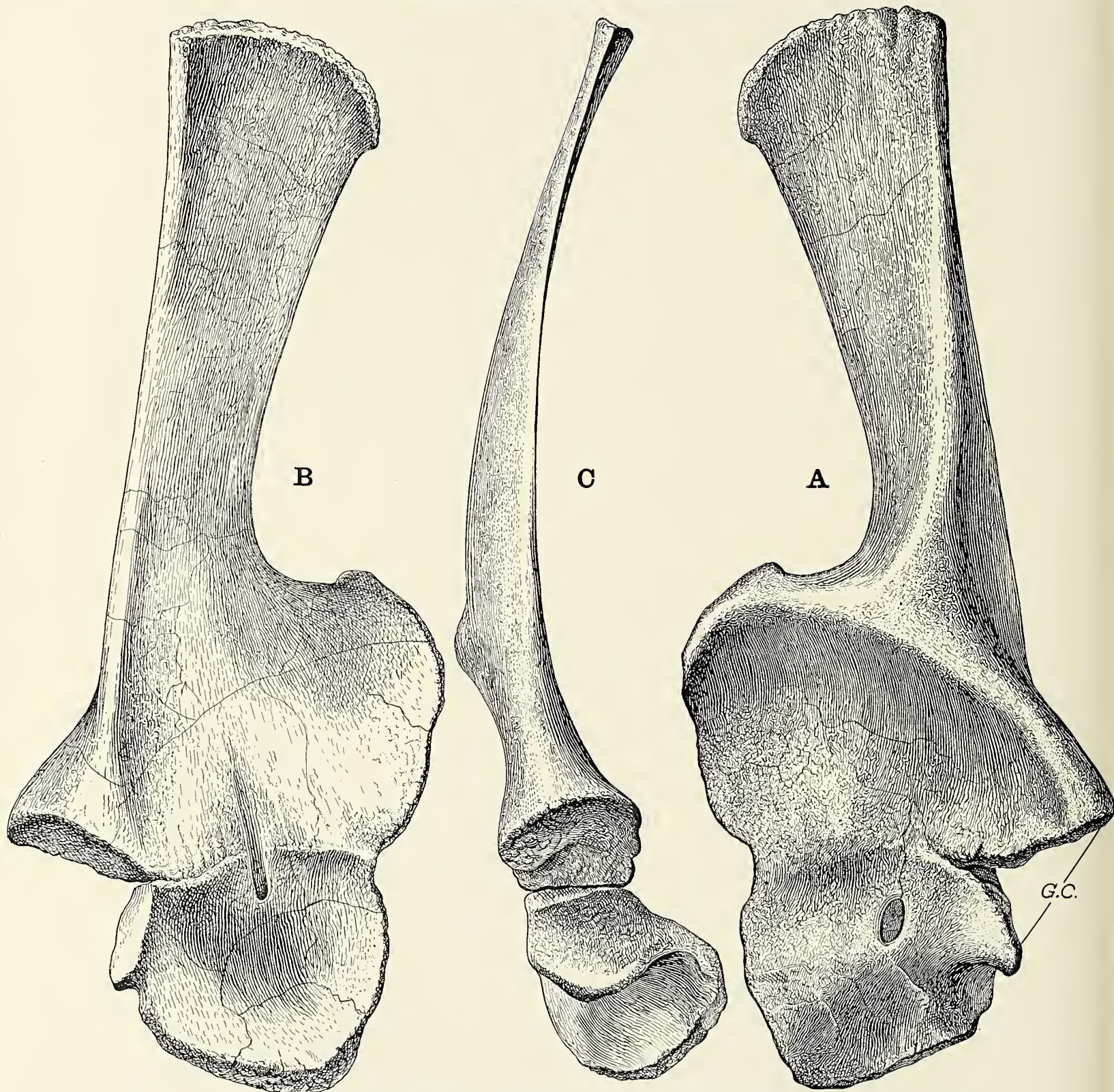


FIG. 9. Left scapula and coracoid of *Apatosaurus louisæ* Holland. Type. No. 3018 C. M. A., external view; B., internal view; C., posterior view; G.C., glenoid cavity. One-tenth natural size.



end in the anterior direction. The surface of the upper end is rugosely roughened probably for the attachment of a suprascapula. The external surface of the blade is irregularly convex, the internal slightly concave. Both anterior and posterior borders thin out to sharp edges. The sharp edge of the posterior border continues downward to the backwardly inclined portion to form the glenoid cavity near the lower end, where the bone thickens transversely, see C, fig. 9. The scapula of *A. louisæ* may be distinguished at once, by the narrowness of the distal extremity of the blade, and the straightness of its posterior border, from such forms as *Diplodocus*, *Haplocanthosaurus*, and *Camarasaurus*, all of which have a double expansion of this end. From *Alamosaurus* it may be separated by the relatively narrower blade and the higher and more oblique position of the transverse ridge. The straightness of the posterior border of the blade, the reduced area of the superior

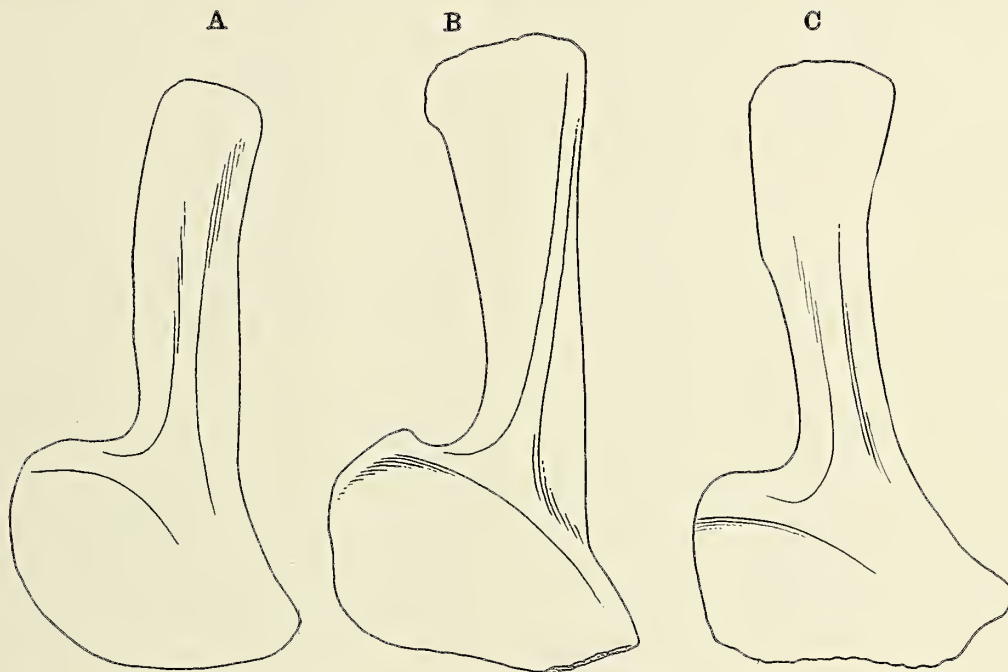


FIG. 10. Comparative outline views of *Apatosaurus* scapulæ. A., left scapula of *A. ajax*, Type; B., same of *A. louisæ*, Type; C., same of *A. excelsus*, Type. All figures about one-twenty-fourth natural size.

muscular fossa, and the diagonal trend of the transverse ridge, are features that seem to distinguish the scapula of *A. louisæ* from that of *A. excelsus*, see fig. 10.

*Coracoid*.—The coracoid of *A. louisæ* is subrectangular in outline, its vertical and longitudinal diameters being subequal. The whole bone is massive, with an irregularly convex outer, and a concave inner surface. It is much thickened about the glenoid cavity. The coracoid is perforated by a large elliptical foramen that passes diagonally backward through the bone, see fig. 9, emerging on the inner

side close to the coraco-scapula suture about midway between the glenoid and anterior borders.

The anterior and inferior margins are relatively thin. Between the inferior margin of the glenoid cavity and the inferior border there is a shallow notch in the posterior border of the coracoid.

#### COMPARATIVE MEASUREMENTS OF SCAPULÆ AND CORACOIDS

	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.
Greatest length of combined scapula and coracoid . . . . .	2020	...
Greatest length of scapula . . . . .	1640	1660e
Greatest breadth of scapula . . . . .	820	840
Least breadth of scapula . . . . .	240	265
Greatest breadth top of scapula . . . . .	400	...
Length of coracoid . . . . .	370	...
Greatest expanse of glenoid cavity . . . . .	325	...

e = estimated.

#### FORE LIMB.

The left fore limb was found articulated as shown in fig. 3, but of the right leg only the humerus was recovered.

*Humerus*.—The humerus resembles that of *Camarasaurus*, the bone being stout and heavily built. It presents a constricted shaft with expanded ends, the proximal to a much greater extent than the distal end. The deltoid ridge is prominently developed, extending along the anterior external border from the proximal end for one half its length. The anterior face of the upper half of the humerus is broadly hollowed out transversely. The proximal end is convexly rounded from side to side. The head is placed midway between the internal and external borders, but a little nearer to the former and is directed more strongly backward than in *Diplodocus*. Its surface is very rugose. The transverse diameter of the distal end is about twice that of the fore and aft diameter. Viewed from the end it is sub-rectangular in outline, see D, fig. 11. The articular surface is roughly rugose. On the posterior border there is a depression indicative of an anconeal fossa. There is a small, poorly defined, external condyle. The principal characters of this bone are shown in fig. 11. The distal end has a slight inclination forward. Compared with the humeri of *A. excelsus*, see fig. 33, the shaft is more robust and the deltoid ridge is less prominently developed from a proximal view. In all other respects the bones are identical.



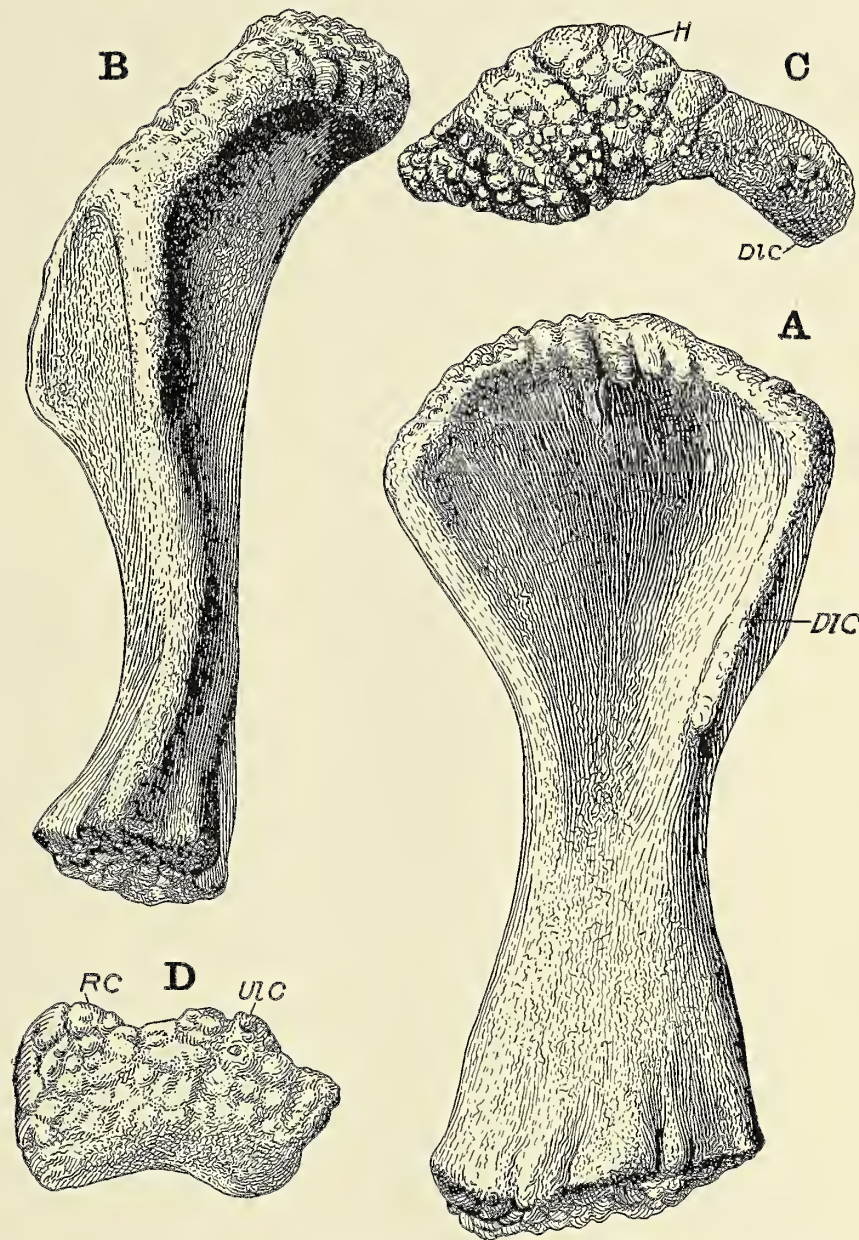


FIG. 11. Left humerus of *Apatosaurus louisae* Holland. Type. No. 3018 C. M. A., anterior view; B., external view; C., proximal view; D., distal view; Dl. C., deltoid crest; H., head; R. C., radial condyle; Ul. C., Ulnar condyle. One-tenth natural size.

COMPARATIVE MEASUREMENTS OF HUMERI

	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.
Greatest length.....	1150	1100
Greatest transverse diameter at proximal end.....	575	600
Greatest transverse diameter at distal end.....	415	410
Least transverse diameter of shaft.....	238	210
Ratio of length of humerus to length of femur.....	.69	.64



*The radius and ulna.*—The radius and ulna of the left fore limb were found articulated and these furnish corroborative evidence of the correctness of Hatcher's<sup>29</sup> determinations as to the proper articulation of these bones. That is, the proximal end of the radius is entirely enclosed by the ulna, posteriorly, see C, fig. 13, and thus the two elements did not cross, as first thought by some paleontologists, but remain more or less parallel in the articulated limb. The radius and ulna are subequal in length, the distal third of the ulna more slender than the corresponding part of the radius.

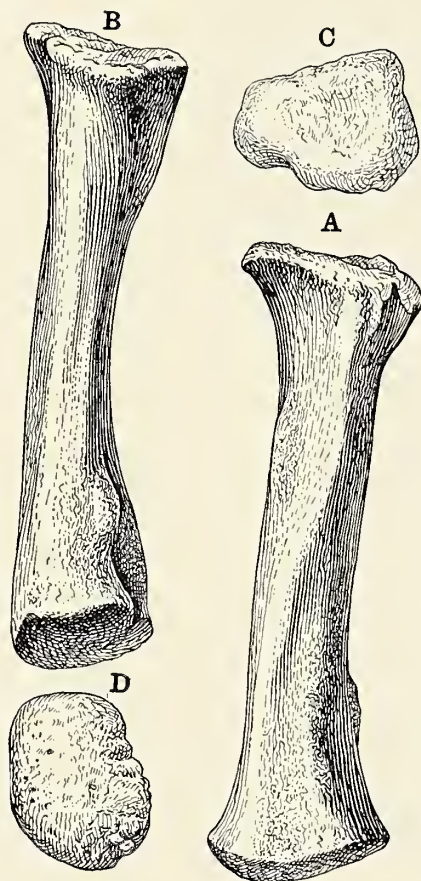


FIG. 12. Left radius of *Apatosaurus louisæ* Holland. Type. No. 3018 C. M. A., anterior view; B., external view; C., proximal view; D., distal view. One-tenth natural size.

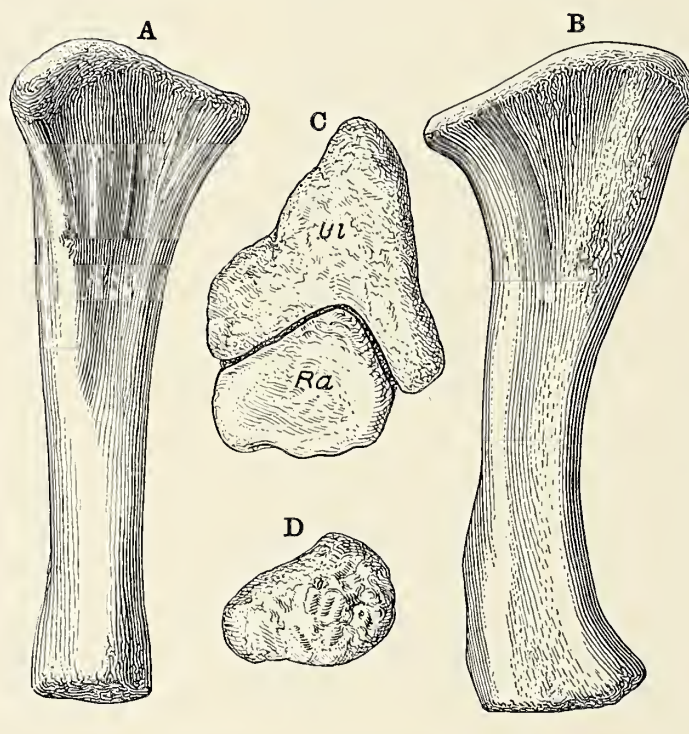


FIG. 13. Left ulna of *Apatosaurus louisæ* Holland. Type. No. 3018 C. M. A., anterior view; B., external view; C., proximal ends of radius and ulna as found articulated; D., distal end of ulna; Ra., radius; Ul., ulna. One-tenth natural size.

The radius has a slightly constricted shaft with subequally expanded ends. The proximal, see C, fig. 12, is slightly concave with a rugose surface. Distally there is a prominent rugosity on the posterior side near the external border. Opposite on the internal side of the ulna a similar rugosity near the distal end is

<sup>29</sup>Hatcher, J. B., Ann. Carnegie Museum, I, 1902, p. 363.

developed, and this doubtless indicates the points of attachment of important ligaments which bound these bones together. On the posterior surface near the distal end, the radius is hollowed out by a longitudinal groove which may have transmitted an artery. The distal end of the radius is subovate in outline with a convex rugose surface.

Viewed from above, see C, fig. 13, the ulna is triangular in outline with a deep concavity in front for the reception of the angularly rounded head of the radius. There is no olecranon process. The ulna gradually reduces in size toward the distal end which is subovate in outline and relatively smaller than the distal end of the radius. On the inner or radial side of the ulna, near the distal end, is a fossa for the reception of the rounded, posterior, external angle of the radius.

#### COMPARATIVE MEASUREMENTS OF RADIUS AND ULNA

	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.
Greatest length of radius.....	800	755
Transverse diameter of radius at distal end.....	232	230
Fore and aft diameter of radius at distal end.....	118	105
Transverse diameter of radius at proximal end.....	240	240
Fore and aft diameter of radius at proximal end.....	180	95
Transverse diameter of radius at middle of shaft.....	125	127
Greatest length of ulna.....	850	740
Transverse diameter of ulna at distal end.....	170	155
Transverse diameter of ulna at proximal end.....	225	330

#### CARPUS.

The carpus in *A. louisæ*, as in *Diplodocus*, consists of a single flattened bone of somewhat irregular shape. It has a rough resemblance to the scapho-lunar described by Hatcher<sup>30</sup> of specimen No. 563 C. M., but is thicker and more block-like. Viewed from above it is subrectangular in outline, thinning out toward the front and internal or radial side, and thickening toward the back. External to the antero-posterior line of greatest thickness, the bone abruptly thins to a small projecting lip that has a slightly concave upper surface that in articulation probably underlay the inner side of the distal end of the ulna. Internal to the antero-posterior line of greatest thickness the surface slopes off quite regularly to the inner margin. The posterior half of this surface is smooth and slightly concave, the

<sup>30</sup>Hatcher, J. B., Annals Carnegie Museum, Vol. I, 1902, pp. 366-367.



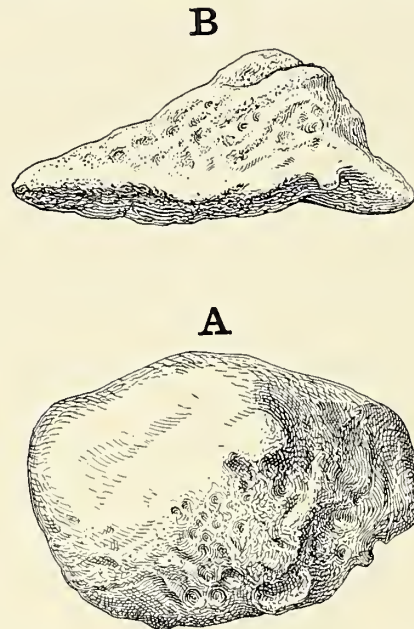


FIG 14. Left scapho-lunar of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., superior view; B., posterior view. One fourth natural size.

anterior half rugosely roughened. If the surfaces have been correctly interpreted, this larger inner surface would lie below the distal end of the radius.

The ventral side of the scapho-lunar<sup>31</sup> is nearly flat with an irregularly roughened surface. If properly articulated on the skeleton, as it seems to be, it is in articulation with metacarpals II, III, and IV. The principal features of this bone are clearly shown in fig. 14.

#### COMPARATIVE MEASUREMENTS OF SCAPHO-LUNAR

	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.
Greatest transverse diameter.....	207	203
Greatest fore and aft diameter.....	140	155
Greatest thickness.....	80	55

<sup>31</sup>In *Camarasaurus* (*Morosaurus*), Osborn (Bull. Amer. Mus. Nat. Hist., Vol. XX, 1904, p. 182) found two carpal elements, the larger of which appears to fit by distinct facets on top of Mtc. I and Mtc. II. From this discovery he concludes these bones represent the coalesced carpalia of the distal row. If this is the correct interpretation, instead of being the scapho-lunar (radiale+intermedium) this single carpal element in *Apatosaurus* would represent coalesced carpalia 1, 2, and 3 of the distal row of the carpus. For the present, however, I shall continue to use the original designation.



## MANUS.

The left fore foot is the only one preserved and was found in position in the matrix at the extremity of the completely articulated fore limb as shown in fig. 15. Metacarpals, I, II, III, IV, and V were in regular order interlocked at their proximal ends. The position of metacarpals I and II in relation to metacarpals III, IV, and V is such as to indicate that the proximal ends of these bones were arranged in the arc of a circle and thus were better adapted to sustain the great weight imposed upon them. In addition to the metacarpals, proximal phalanges of digits I and II were found nearly in position, as was the single large ungual of the first digit and a small sesamoid-like element in close proximity to the distal extremity of the proximal phalanx of the second toe. The other phalangeals are all missing from this foot.

The presence of a single ungual gives further support to the idea that in the manus of the Sauropodous dinosauria there is but a single clawed ungual. On the mounted skeleton the fore feet have been restored with additional phalangeals and

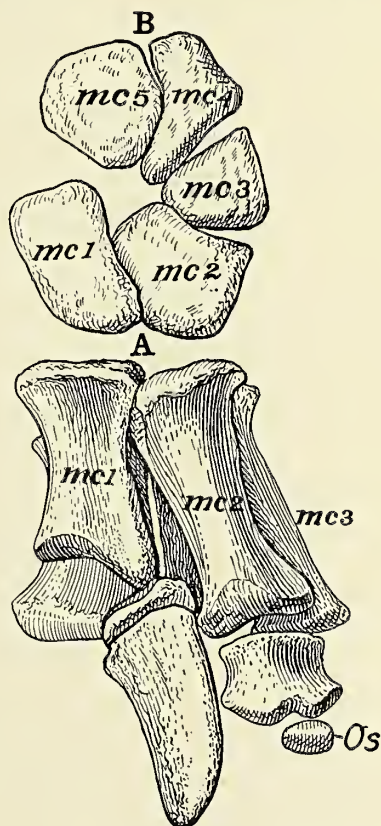


FIG. 15. Left fore foot of *Apatosaurus louisae* Holland. Type. No. 3018 C. M. A., Showing the bones of the manus as found in the matrix. B., Proximal ends of the metacarpals as found. Mc 1, mc 2, mc 3, mc 4, and mc 5, metacarpals one to five. About one-ninth natural size.

unguals on digits II and III respectively. In view of the fact that a considerable number of articulated fore feet of the Sauropoda are now known and that none has been discovered with more than a single clawed ungual in association, the negative evidence thus accumulated seems to indicate there was only one, and that the foot as restored is in error in that respect. Until a manus is found having additional unguals in position, or at least in close association, it is my belief that there is no justification at this time for the addition of extra claws. Some uncertainty also exists as to the precise number of phalanges composing the complete *Apatosaurus* fore foot. The most perfect manus yet known is the one described by Hatcher (Annals Carnegie Museum, vol. I, 1901, pp. 366-374) see fig. 35, which has a complete proximal row of phalanges, a clawed ungual on digit I, and a sesamoid element whose exact position may still be considered uncertain although found on the palmar side of the foot lying between the distal end of mc. III and its proximal phalanx. The presence of a similar element at the end of the proximal phalanx of digit II in the present specimen leads to the suggestion that perhaps these ossicle-like elements are not sesamoids but represent the remnants of degenerating toe bones, nothing more than functionless ossicles, similar to those found in practically the same position on digits IV and V of the pes in both *Apatosaurus* and *Diplodocus*.

The phalangial formula of *Apatosaurus* as positively known at the present time is 2, 1, 1, 1, 1, or if the ossifications are phalangial remnants as has been suggested, the formula would be 2, 2, 2, 1, 1, a more probable arrangement. It will be only by the discovery of more completely preserved feet that the point raised can ever be established.

The whole structure and arrangement of the metacarpus and phalanges is so modified as to indicate that the principal weight of the body was supported by the manus on the inner side of the foot.

*Metacarpals.*—The metacarpal bones of *A. louisæ* so closely resemble those of *A. excelsus* (No. 563 C. M.) described in detail by Hatcher (see pages 257 to 260) that at this time it appears only necessary to call attention to those features in which they differ.

The metacarpals of *A. louisæ* are normal uncrushed bones, whereas the pes of *A. excelsus* No. 563 C. M. has suffered from vertical compression, and the articular ends have been considerably altered by this crushing, a condition for which Hatcher made some allowance in his description.

Metacarpal I of No. 3018 C. M., except for its slightly larger size, corresponds closely in all of its main characteristics with the first metacarpal of No. 563 C. M.

The articular ends of the last mentioned bone have been much compressed



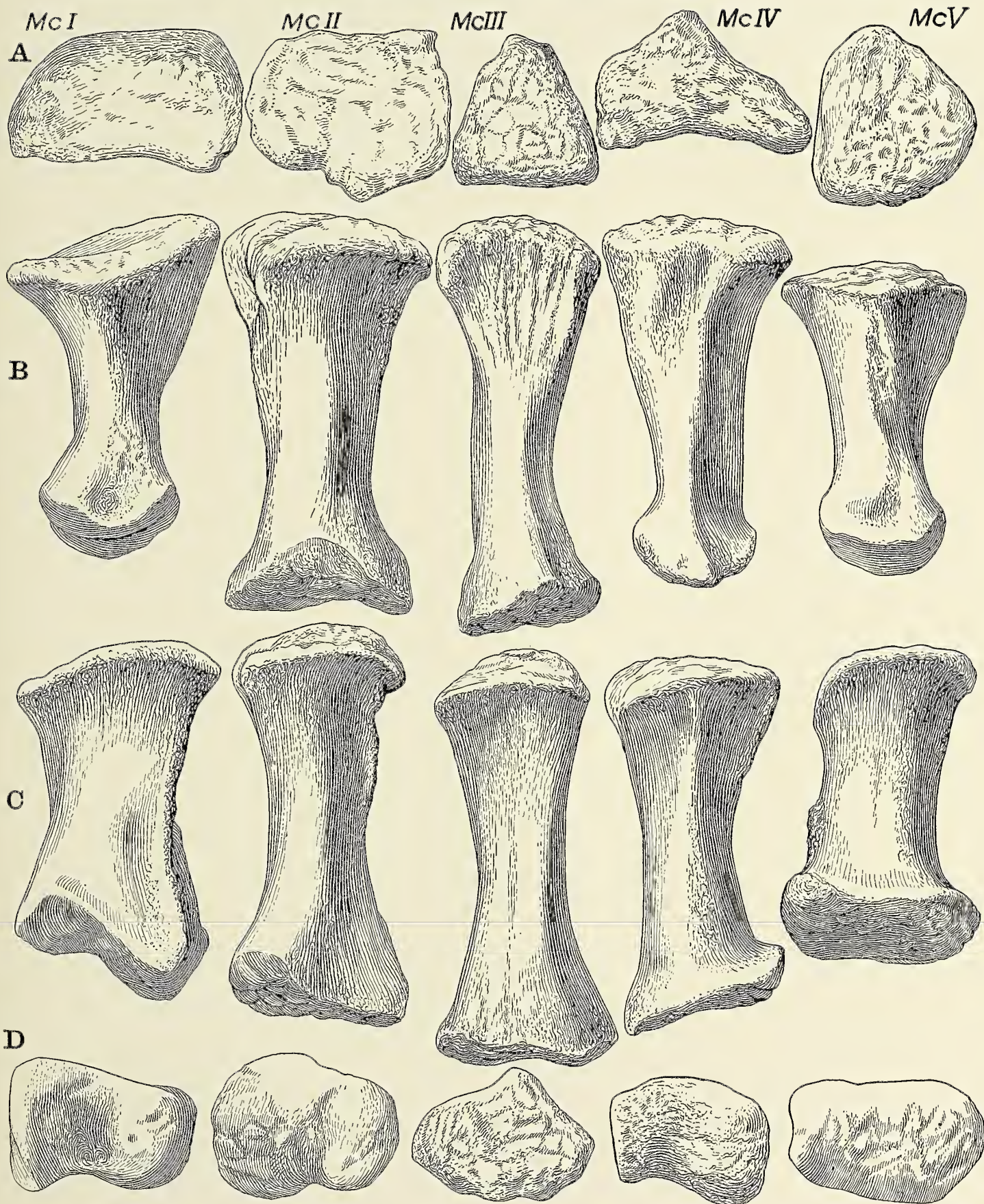


FIG. 16. Left metacarpals of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., proximal views; B., lateral views; C., anterior views; D., distal views. Mc. I, Mc. II, Mc. III, Mc. IV, Mc. V, metacarpals one to five respectively. All one-fourth natural size.



which will in great measure account for the considerable differences shown in the diameters of the articular ends of these bones in the table of comparative measurements.

Metacarpal II has the proximal end deeper than wide, whereas, due to crushing, metacarpal II of No. 563 C. M. is wider than deep. The surface of this end is regularly convex in all directions. A plane passed through the greatest diameter of the proximal end would bisect the line of greatest diameter of the distal end at an angle of nearly 45 degrees. In this same bone of No. 563 C. M. these two diameters are in the same transverse plane. The distal end is broader than deep, the surface being regularly convex vertically, and shallowly concave transversely. The outline of the uncrushed proximal end is well shown in A, fig. 16.

Metacarpal III, except for the more robust character of the articular ends, is in close accord with the third metacarpal of No. 563 C. M., described in detail on page 259.

The uncrushed proximal end of metacarpal IV is subtriangular in outline, see A, fig. 16, the lines bounding the internal and superior borders are subequal in length and meet at right angles. The hypotenuse of this triangle is formed by the regularly concave line of the outer border. The inner border is shallowly indented for articulation with Metacarpal III, not deeply emarginated as in Metacarpal IV of No. 563 C. M., a condition plainly exaggerated by vertical crushing. In all other respects the two bones are in agreement.

Metacarpal V is the shortest bone of the series, but very stout in this specimen. In outline the proximal end is subround, see A, fig. 16, the articular surface being convex in all directions. This end of No. 563 C. M. is crescentic in shape, and entirely unlike Metacarpal V of No. 3018 C. M., though doubtless the former has been somewhat altered by crushing. The inner side of Metacarpal V of No. 3018 C. M., at the proximal end, presents a flattened surface for articulation with Metacarpal IV. The superior or front surface of this element, see fig. 16, is broad and gently convex transversely. The distal end is expanded in all directions. Viewed from the end it is quadrangular in outline, with the longest diameter transverse, as contrasted with the subround end of the fifth metacarpal of No. 563 C. M.

Such differences as have been found in the metacarpal bones of these two specimens may for the most part be attributed to distortion brought about by the vertical crushing to which the manus of No. 563 C. M. has been subjected. With the exception of Metacarpal V all of the other elements are in close accord.

*Phalanges*.—The proximal phalanx of digit I of *A. louisæ* differs from the same bone of No. 563 C. M. in the lack of a palmar flange extending backward under the distal articular end of Metacarpal I. This feature of the No. 563 C. M. bone,

however, is quite certainly exaggerated by crushing. In all other respects the two bones are very similar.

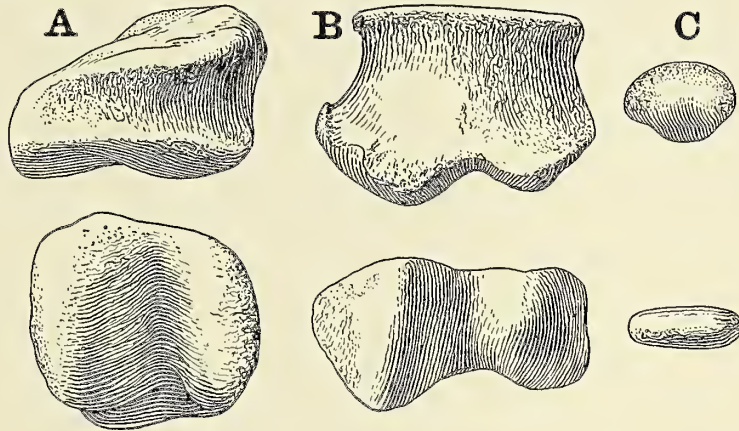


FIG. 17. Phalanges of left fore foot of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., proximal phalanx, digit I; B., proximal phalanx, digit II; C., Ossicle-like phalanx found at distal end digit II. All one-fourth natural size.

The proximal phalanx of digit II is in full accord with the corresponding element of specimen No. 563 C. M.

The ungual phalanx of digit I differs so entirely from the homologous bone of No. 563 C. M. as to require a detailed description, especially since the pointed ungual of that foot is abnormal, a condition partly recognized by Hatcher at the time of describing it.

This ungual is a deep, compressed, slightly curved bone, with a squarely truncated anterior extremity, see fig. 18. The internal surface is strongly convex from

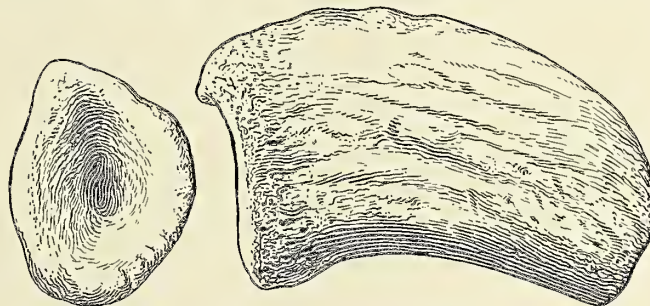


FIG. 18. Ungual phalanx of digit I of left manus of *Apatosaurus louisæ*. Type. No. 3018 C. M. Lateral and end views. One-fourth natural size.

above downward, the external nearly flat. The proximal end is deeply cupped as shown in fig. 18. The truncated anterior end presents a bluntly obtuse edge. The surfaces of the bone are roughened, with the customary longitudinal groove on the lower internal surface. The ungual as a whole is less curved on the ventral border than the unguals of the pes.



The principal dimensions of these bones of the foot are given below in the table of comparative measurements.

## COMPARATIVE MEASUREMENTS OF METACARPALS

Meta- carpal	Greatest length		Greatest transverse diameter proximal end		Greatest transverse diameter distal end		Least diameter of shaft		Greatest diameter antero-posterior proximal end	
	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
I	265	257	100	80	147	103	69	70	175	155
II	285	285	130	122	140	149	77	80	152	85
III	293	285	113	110	130	119	59	70	115	74
IV	245	240	125	76	124	110	62	60	130	125
V	235	232	130	68	144	110	68	57	137	142

## MEASUREMENTS OF PHALANGIALS

	Length		Greatest breadth		Greatest depth proximal end		Greatest depth distal end	
	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Proximal phalanx, digit I. .	76	75	120	105	95	85	90	83
Proximal phalanx, " II.	100	90	138	138	99	100	76	75
Proximal phalanx, " III	...	67	...	130	...	65	...	23
Proximal phalanx, " IV	...	68	...	109	...	66	...	42
Proximal phalanx, " V.	...	75	...	125	...	70	...	52
Ungual, digit one . . . . .	215	205	95	64	130	125	...	...

## THE PELVIS.

All of the pelvic bones are present in specimen No. 3018 C. M. and were found in articulated position with the sacrum. The coössification of the pubes with the ischia, and the further coössification of the latter with each other at their distal ends, establishes beyond question the true relationships of the bones forming the pelvic girdle. The pubes and ischia in the mounted skeleton are more divergent than first indicated by Marsh, but they are in exact accord with the skeleton of *Apatosaurus excelsus* in the Field Museum which has the pubes and ischia similarly coössified.

*Ilium*.—The ilia are both incomplete. The left lacks the anterior process in front of the pubic peduncle and most of the superior crest, the right has the anterior end fairly complete with the exception that much of the upper half is missing.



The illustration shown in fig. 19 has been drawn from both ilia with the superior border restored from No. 563 C. M., which has the left ilium completely preserved as shown in fig. 36. Below on the inner side it articulates with the five coalesced

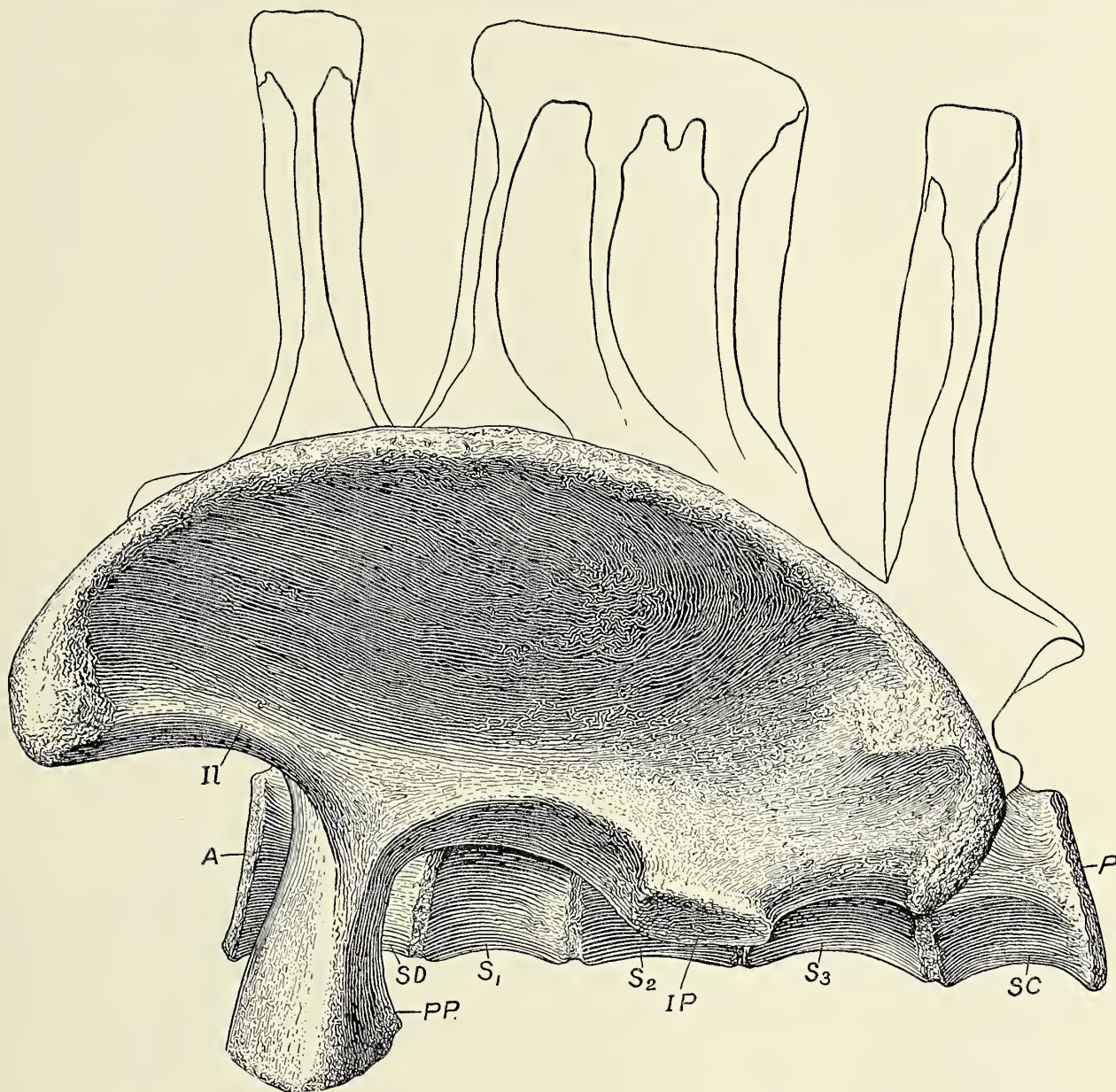


FIG. 19. Left ilium and sacrum of *Apatosaurus louisæ*. Type. No. 3018 C. M. Viewed from the left side. The ilium partly restored from the right. A., anterior end; Il., ilium; I.p., ischiac peduncle; P., posterior end; P.p., pubic peduncle; S.c., sacrocaudal; S.d., sacrodorsal; S.1, S.2, S.3, primary caudals one to three. One-tenth natural size.

sacral ribs and the corresponding diapophyses which are now completely hidden in this specimen. The ilium is produced far in front of the pubic peduncle into a



broad but gradually narrowing anterior blade. This anterior blade is obtusely pointed as in *Diplodocus*, not broad as in *Haplocanthosaurus*. The lower border of the blade forms nearly a right angle with the anterior border of the pubic peduncle, as in the type of *B. excelsus* in contrast to the acute angle found in other specimens of the latter species.

*Pubis*.—The pubes are proportionally short and stout with expanded ends, especially the proximal. They are much thickened at the acetabular border. The pubis articulates proximally with the great peduncle of the ilium and laterally with the ischium by a long, nearly vertical suture that extends downward from the acetabulum. This suture is fully coalesced on both sides. The distal ends are moderately enlarged; they are united, probably by cartilage, on the median line

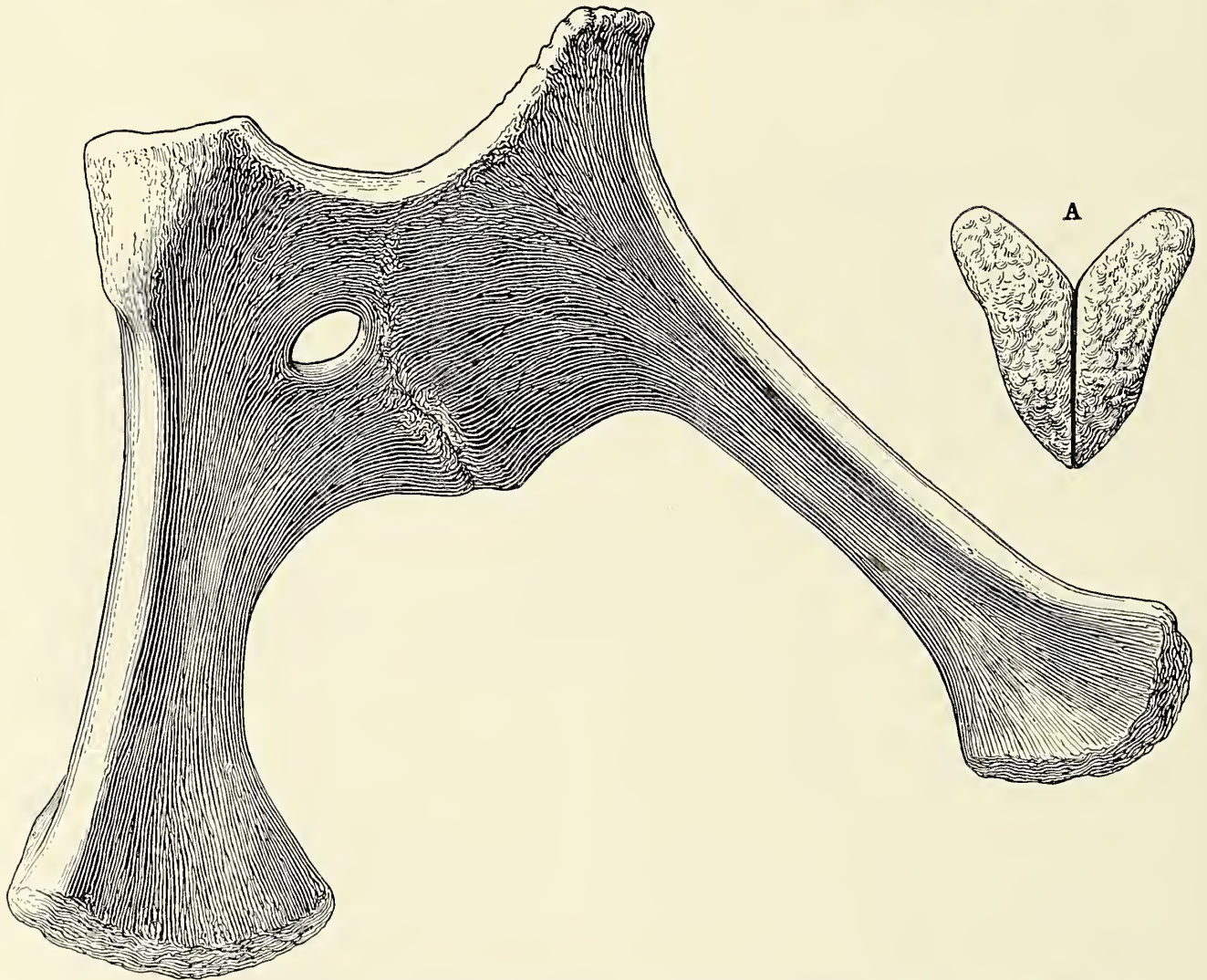


FIG. 20. Left coössified ischium and pubis of *Apatosaurus louisæ*. Type. No. 3018 C. M. Lateral view; A., coössified distal ends. One-tenth natural size.

and again at a point at their midlength. An elongated slot separates the inner borders between these two points of contact. A pubic foramen opens downward immediately below the anterior border of the acetabulum. The end for articulation with the greater peduncle of the ilium is concave. The broadly expanded proximal ends of the pubes are concave internally and convex externally.

*Ischium*.—The ischia of *Apatosaurus* are longer and more slender than the pubes. The broadly expanded proximal end presents two articulating surfaces, an upper that unites by cartilaginous union with the lesser peduncle of the ilium, a lower with the pubis by the anterior margin of the blade. Between the two articular surfaces the border is concave antero-posteriorly and contributes to the boundary of the acetabulum. Posterior to the proximal end the shaft curves strongly mesial to meet its fellow of the opposite side on the median line, at about midlength.

In this specimen the two ischia are firmly coössified throughout the length of this contact. The distal end is somewhat expanded but more especially on the posterior side. Viewed from the end the cojoined ischia present a heavy U-shaped termination with rugosely roughened surfaces. See A., fig. 20.

#### COMPARATIVE MEASUREMENTS OF PELVIC BONES

	<i>A. louisæ</i> No. 3018 C. M.	<i>A. excelsus</i> No. 563 C. M.
	mm.	mm.
<b>ILIUM</b>		
Length over all.....	1460	1280
Acetabulum to superior border about.....	570	450
Diameter from pubic to ischiac peduncle.....	460	445
<b>PUBES</b>		
Length over all.....	1190	950
Greatest breadth of proximal end.....	...	425
Greatest breadth of distal end.....	270	300
Least breadth of shaft.....	105	150
<b>ISCHIA</b>		
Length over all.....	1275	1075
Greatest breadth of proximal end.....	500	600
Greatest breadth of distal end.....	335	300
Least diameter of shaft.....	105	100
Transverse diameter of coalesced distal ends.....	345	...

#### HIND LIMB.

The hind limbs are represented by the right femur, tibia, fibula, and astragalus, and the greater portion of the left pes.



*Femur*.—The right femur is almost perfectly preserved and being free from distortion gives a perfect idea of the shape and proportions of this important bone.

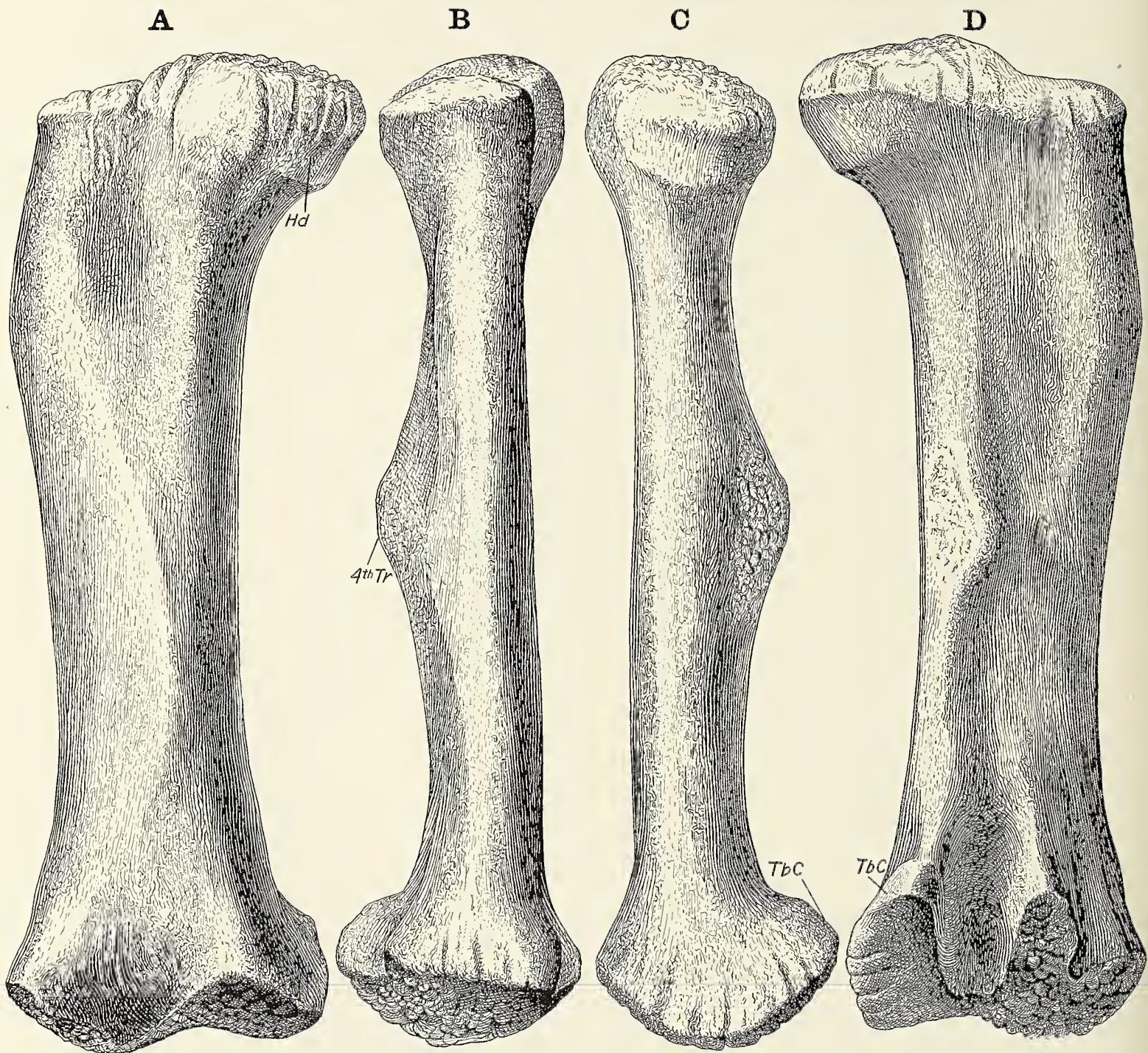


FIG. 21. Right femur of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., front view; B., external view; C., internal view; D., back view; Hd., head; Tb.c., tibial condyle; 4th tr., fourth trochanter. One-tenth natural size.



The femur is a stout bone, in fact stouter than in any other known member of the Sauropoda except the unusually stout-limbed *A. amplus* Marsh. The head is rugosely roughened and rises above the level of the great trochanter. The shaft in cross-section is flattened antero-posteriorly and widened transversely so that in cross-section it would be ovate in outline. As in other Sauropod femora, the head is not distinctly separated from the shaft but the rugose surface of the latter is continued uninterrupted and covers the superior surface of the great trochanter. The fourth trochanter exists as a strongly developed ridge, developed on the postero-internal angle of the shaft, and located somewhat above midlength. In *Diplodocus*, Hatcher erroneously designates this as the third trochanter. In *Camarasaurus*, Osborn and Mook (Mem. Amer. Mus. Nat. Hist., III, pt. 3, 1921, p. 365) point out that the apex of the fourth trochanter is exactly at midlength of

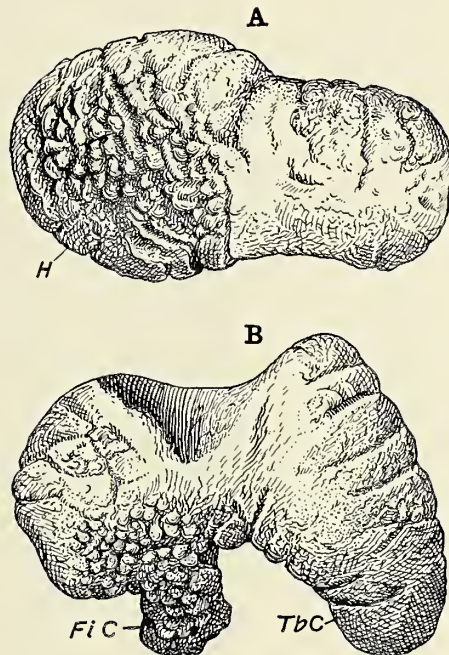


FIG. 22. Articular ends of femur of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., proximal end; B., distal end; *Fi.C.*, fibular condyle; *H.*, head; *Tb.C.*, tibial condyle. One-tenth natural size.

the bone. This may, however, be only an individual characteristic. The external and internal condyles are separated by a deep intercondylar groove the inner one being much the larger. The outer one is cleft by a deep, fibular groove. Compared with the femur of the Field Museum *Apatosaurus* specimen the closest resemblances are found throughout. The principal features of this bone are clearly shown in figs. 21 and 22.



	No. 3018 C. M.	No. 563 C. M.	No. 7163 F. M.
	mm.	mm.	mm.
Greatest length.....	1785	1710	1830
Greatest breadth at proximal end.....	575	543	570
Greatest breadth at distal end.....	565	515	590
Least diameter of shaft.....	320	260	310

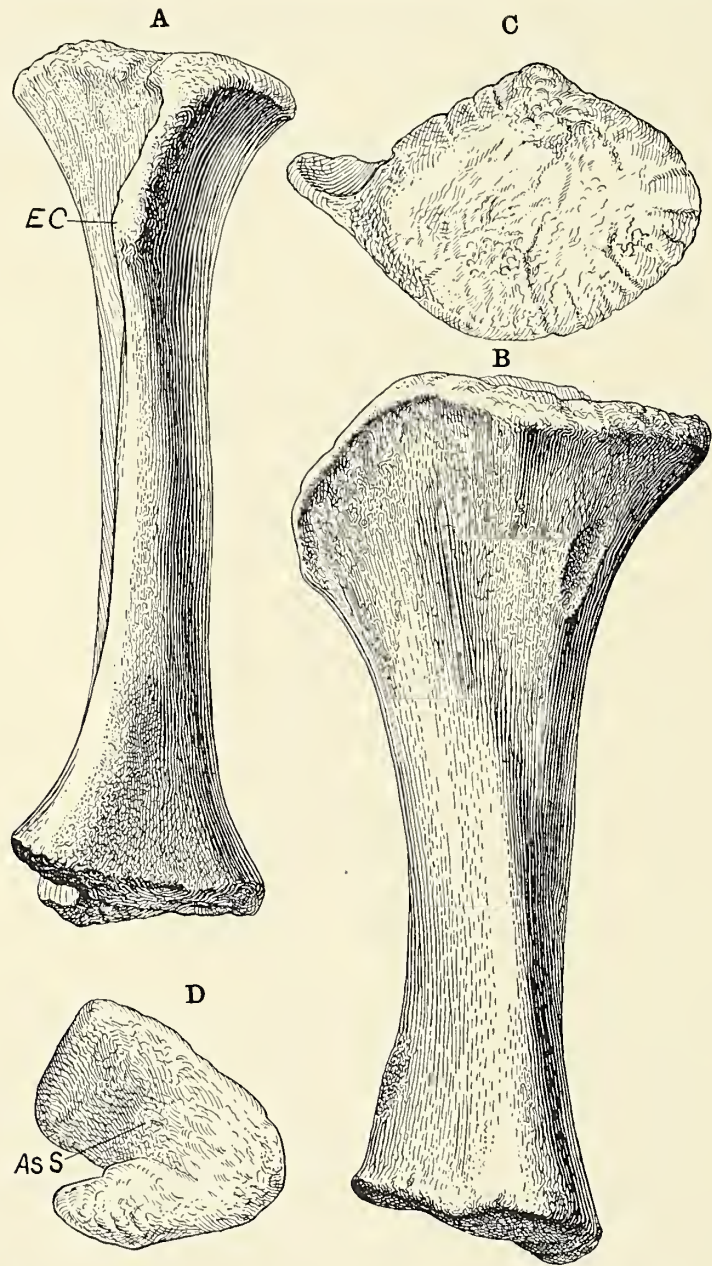


FIG. 23. Right tibia of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., front view; As.S., articular surface for astragalus; B., internal view; C., proximal end view; D., distal view; E.c., enemial crest. One-tenth natural size.

*Tibia and fibula.*—The right tibia and fibula preserved with specimen No. 3018 C. M. are hardly to be distinguished from the corresponding bones of *Camarasaurus*, although both can be readily differentiated from the lower limb bones of the more slender *Diplodocus*.

The tibia of *Apatosaurus* is considerably shorter than the femur. The proximal end is more expanded than the distal principally in a transverse direction. The thick enemial crest is located on the anterior internal angle and partly locks the fibula in position. Viewed from above, see C, fig. 23, the proximal end is angularly rounded the entire surface being rugosely roughened. The shaft of this bone is

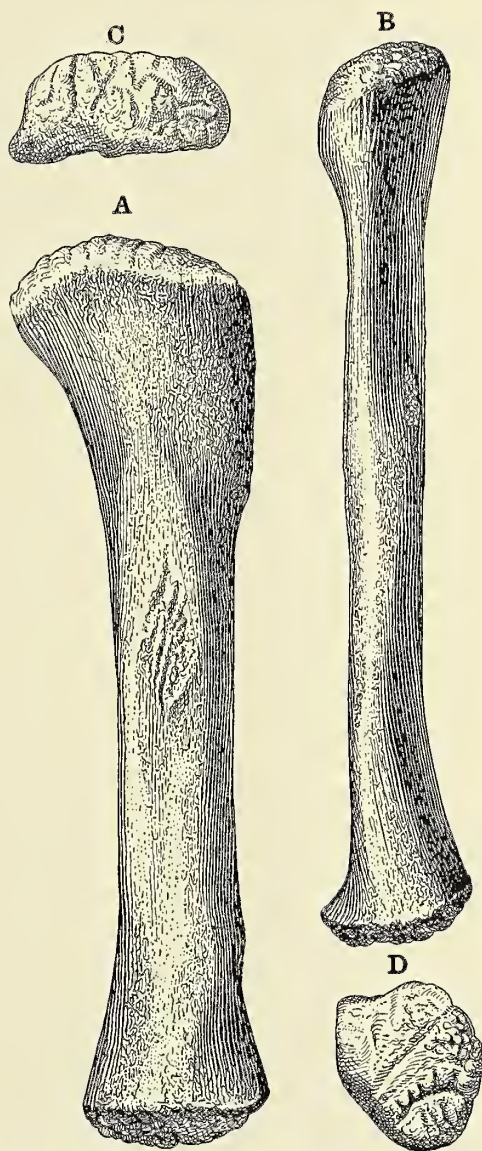


FIG. 24. Right fibula of *Apatosaurus louisae*. Type. No. 3018 C. M. A., lateral view; B., posterior view; C., proximal end view; D., distal end view. One-tenth natural size.



comparatively thick, but constricted in regard to the ends. On its internal and posterior distal extremity it sends downward an internal malleolus that is separated from the main shaft of the bone by a vertical groove for the transmission of the tendons of the muscles of the foot. This process is in articulation with the posterior and internal surface of the astragalus. The features of this bone are clearly set forth in fig. 23.

The fibula is much more slender than the tibia and exceeds it in length. When in an articulated position it extends well below the distal end of the tibia and abuts against the outer side of the astragalus. As in *Diplodocus* it has displaced the calcaneum and nearly reaches the proximal ends of metatarsals IV and V. The proximal end is slightly expanded antero-posteriorly but the width of the shaft remains subequal throughout its length, see fig. 24, with very slight enlargement of the distal end. The whole bone is flattened transversely but more especially on the inner side of the proximal end where it articulates with the tibia. A thinned anterior edge fits into the broad groove formed by the recurved enemial crest of the tibia. On the external surface of the fibula, slightly above its midlength, is a vertically ovate roughened area indicating a point of insertion for a large muscle. The distal end of this bone is subround in outline. The internal side of this end in articulation projects inward beneath the tibia to meet the astragalus.

#### COMPARATIVE MEASUREMENTS OF TIBIA AND FIBULA

	No. 3018 C. M.	No. 563 C. M.
	mm.	mm.
Greatest length of tibia.....	1115	1010
Greatest breadth at proximal end.....	545	445
Greatest breadth at distal end.....	345	348
Greatest length of fibula.....	1175	1095
Greatest breadth at proximal end.....	310	...
Greatest breadth at distal end.....	240	245

#### THE PES.

The hind foot, as represented in specimen No. 3018 C. M., consists of the right astragalus; and the following elements of the left pes; metacarpals I, II, III, and IV; the complete row of proximal phalangials, two phalangials of the second row pertaining to digits II and III; and three unguals. The missing bones have been restored from a complete foot, No. 89 in the Carnegie Museum collections, and thus the digital formula for *Apatosaurus* can now be stated as 3, 4, 5, 3, 2. A rough

measurement of the articulated foot shows it to have a transverse width of about 31 inches, and a length of about 27 inches.

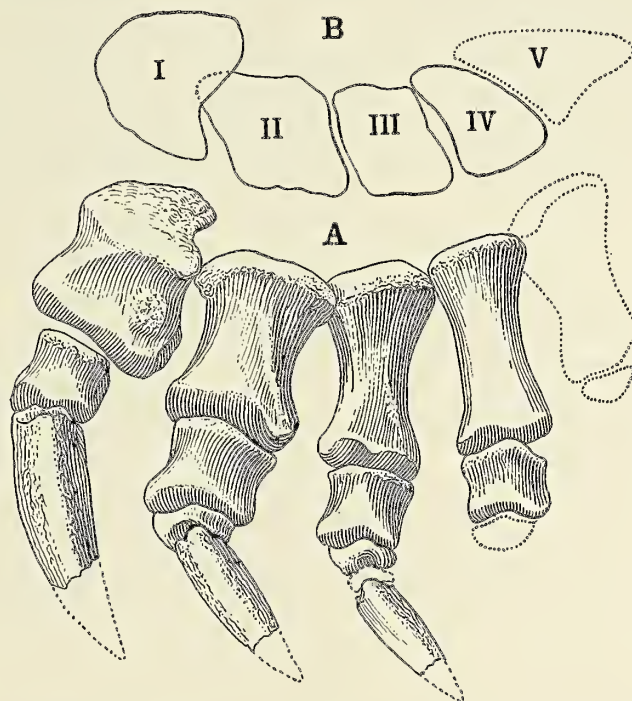


FIG. 25. Articulated hind foot of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., superior view; B., proximal view. Metatarsals one to four. About one-ninth natural size.

*Tarsus*.—The osseous portion of the tarsus in *Apatosaurus* as in *Diplodocus* and *Camarasaurus* consists of the astragalus. In the present specimen this bone was not fused with the distal end of the tibia as often happens in aged individuals, but was found free. It is a heavy, sub-triangular shaped bone, that in the articulated limb is entirely covered superiorly by the distal end of the tibia. The anterior surface of the astragalus presents a broad, regular convex face for the articulation with the proximal ends of metatarsals I, II, and III, and the inner proximal end of metatarsal IV. The external end, the deepest portion, is deeply excavated. A projecting inferior margin having a superior articular surface was opposed by the inner distal end of the fibula. Posteriorly, toward the outer end the astragalus develops a heavy, wide vertical ridge which separates the external cavity from a smaller internal excavation as clearly shown in fig. 26. Inferiorly the astragalus has a broad, rugose, regularly convex plantar surface.

#### MEASUREMENTS OF ASTRAGALUS.

Greatest transverse diameter of astragalus.....	320 mm.
Greatest depth about.....	186 mm.



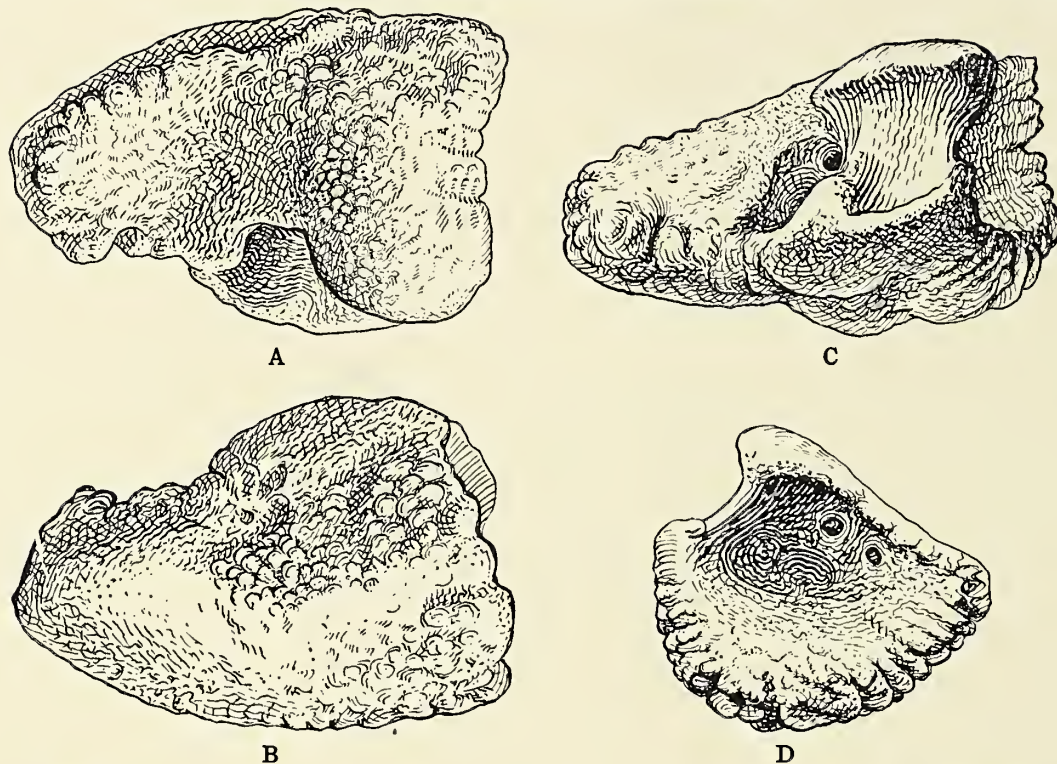


FIG. 26. Right astragalus of *Apatosaurus louisæ*. Type. No. 3018 C. M. A., superior view; B., inferior view; C., posterior view; D., external view. One-fifth natural size.

*Metatarsals*.—The metatarsus is composed of five well developed functional metatarsal bones. Metatarsal I is the shortest and stoutest bone of the series. It is constricted medially, expanded vertically at the proximal and transversely at the distal ends. The articular end surfaces are strongly oblique to one another, converging toward the inner side of the foot. The proximal surface is nearly flat, the distal strongly convex antero-posteriorly. The medial third of this end projects prominently downward from the remainder of this surface as shown in fig. 27. The external lateral margin of the proximal end is deeply concave antero-posteriorly for articulation with the convex internal margin of metatarsal II.

Metatarsal II is slightly longer and less stout than metatarsal I, although decidedly stronger than metatarsal III. It is somewhat constricted both in vertical and lateral diameters. The proximal end is trapezoidal in outline, the distal end subrectangular. A prominent rounded ridge is developed on the front surface and extends diagonally downward to the distal exterior angle. The distal articular end presents a regularly convex articular surface antero-posteriorly, but is concave transversely. This surface is for the accommodation of the low median keel of the proximal phalanx. The detailed features of this bone are clearly depicted in A, B, C, and D, fig. 27.



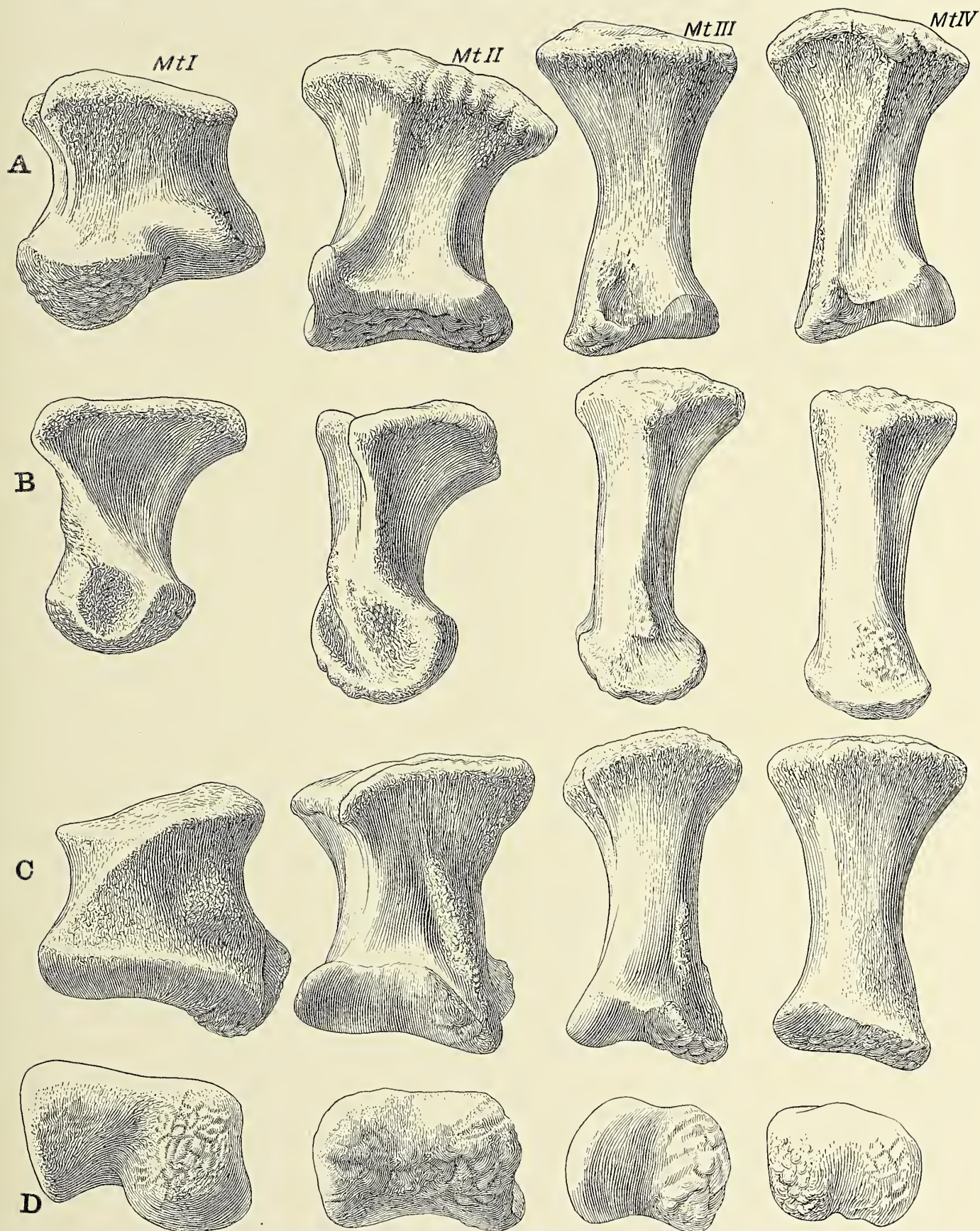


FIG. 27. Left metatarsals of *Apatosaurus louisae*. Type. No. 3018 C. M. A., posterior views; B., external views; C., anterior views; D., distal views. Mt. I, mt. II, mt. III, mt. IV, metatarsals one to four respectively. All one-fourth natural size.



Metatarsal III is the longest of the series and decidedly more slender than metatarsal II. The shaft of this bone is constricted both laterally and antero-posteriorly, more especially in the latter diameter. The outer side of the bone is longer than the inner. The proximal end is subrectangular in outline with the greatest diameter in a fore and aft direction. The distal end is widest transversely with the median surface greatly hollowed out to accommodate the articulation of the proximal phalangeal.

Metatarsal IV is slightly stouter than the preceding element, and of about the same proportions. The proximal articular end is subtriangular in outline. The distal end is subrectangular with a slight grooving of the median area. Just behind the distal part of the bone there is a shallow median depression as shown in A, fig. 27.

Metatarsal V which is missing in the present specimen may be distinguished from all of the others by its greatly expanded proximal and little enlarged distal end.

The manner in which the different elements of the metatarsus articulate at their proximal ends is clearly indicated in B, fig. 25.

*Phalanges.*—All of the phalanges of the left pes are present except the third small phalanx of digit III, the second of digit IV, and the vestigial proximal phalanx of digit V. These missing bones are present in the foot of a second specimen, No. 89 C. M.,<sup>32</sup> and are briefly described in order to make the description complete.

The first digit supports two phalanges. The proximal one is short and deep and articulates distally with the long, compressed, curved claw-like ungual. The proximal end of the first phalanx, see C, fig. 28, is slightly cupped, the distal end broadly grooved vertically. This end is cut off oblique to the longer axis of the bone, so that its articular surface looks somewhat outward. The large ungual of this foot lacks its anterior extremity, but as shown by the ungual of No. 89 C. M., it was obtusely pointed. The lower two-thirds of the articular end is shallowly concave dorso-ventrally, this surface being oblique to the longer axis of the bone, thus causing the ungual to be directed strongly outward when properly articulated. A decided longitudinal groove on its lower internal side, together with the pitted and roughened character of its surfaces, evidently indicates it to have been enveloped in life with a horny sheath which would have materially increased the size of this claw.

Digit II has three phalanges. The proximal is the largest of the entire first row. It is slightly longer than broad, with the inner side nearly perpendicular but the anterior surface slopes downward toward the outer side, which is relatively

<sup>32</sup>See Hatcher, Mem. Carnegie Museum, I, No. 1, 1901, fig. 22.

narrow and rounded. The inner side of the distal end is produced prominently forward thus giving this end a diagonal trend when viewed from above.

The second phalanx of this toe is reduced to a flattened wedge of bone, thickest on the internal side and compressed to an obtuse edge on the external side, see fig. 28. The terminal phalanx of this digit differs chiefly from the ungual of digit one in its smaller size.

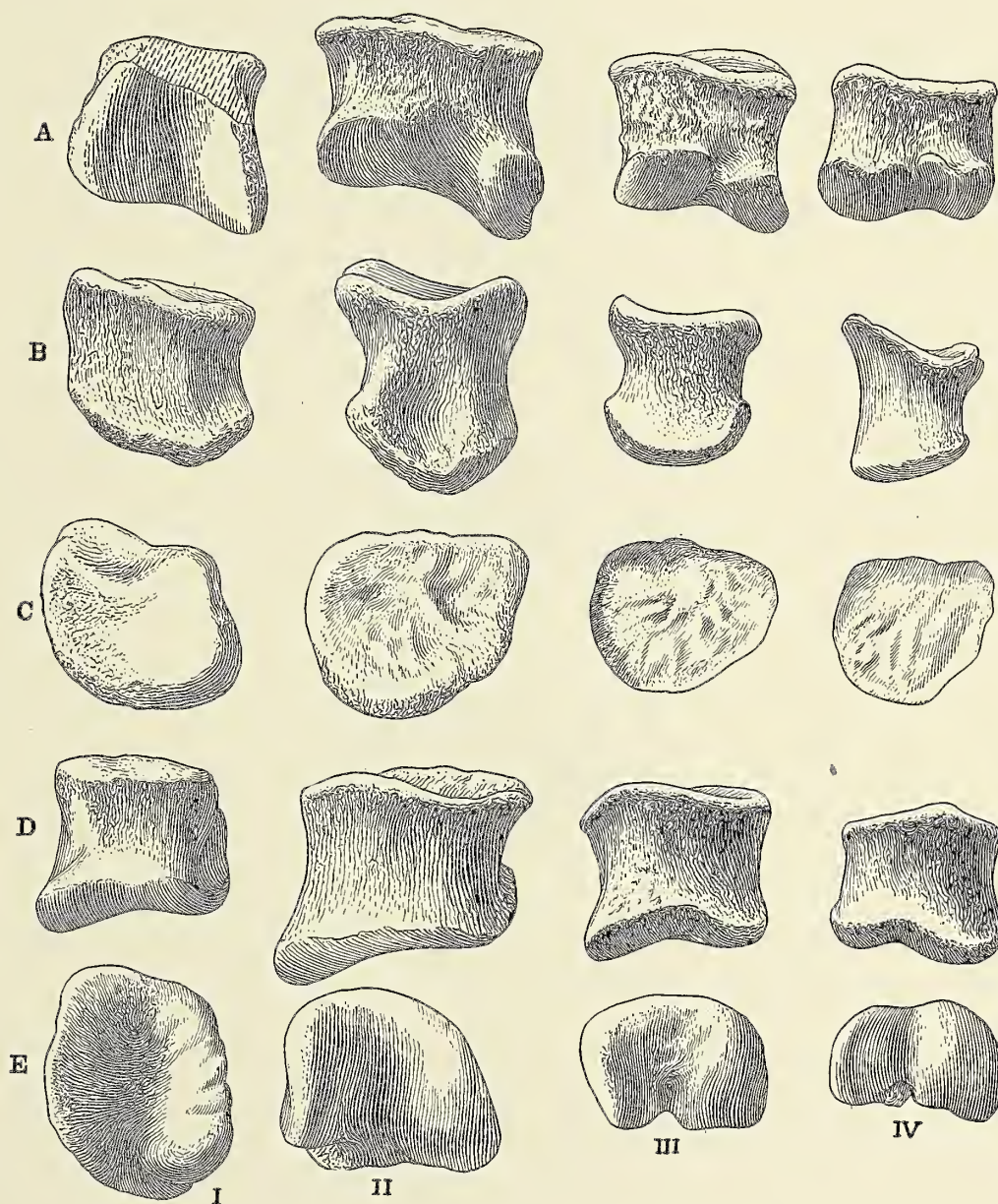


FIG. 28. Proximal row of phalangeals of *Apatosaurus louisae*. Type. 3018 C. M. A., posterior views; B., lateral views; C., proximal views; D., anterior views; E., distal views., I, II, III, and IV, phalanges one, two, three, and four respectively. One-fourth natural size.



Digit III has four phalanges. The proximal is slightly longer than wide, with a concave proximal end and a shallowly grooved distal extremity. The second phalanx is a short, wedged-shaped bone that is thickest on the internal side. The third is missing in this specimen but in the complete pes of No. 89 C. M. it is a very short, ovately rounded, disk-like element. The ungual phalanx of digit III is hardly more than half the size of the claw on the first toe, but otherwise resembles it closely, see fig. 30.

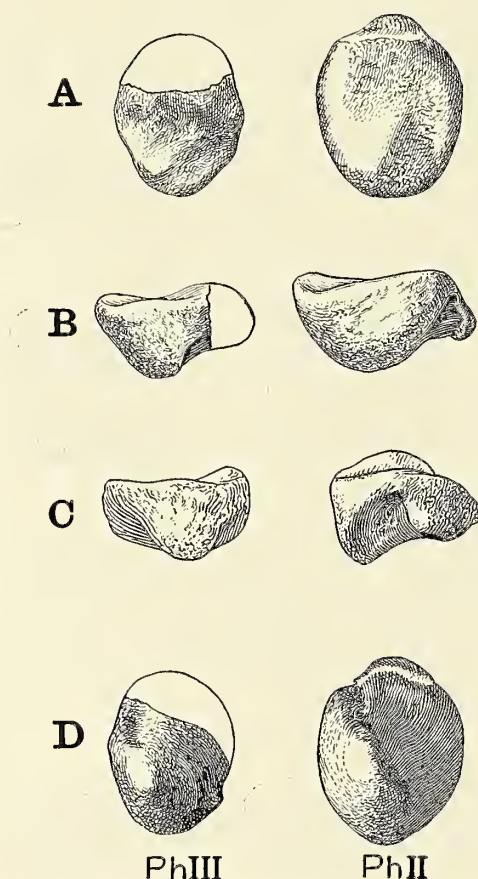


FIG. 29. Phalanges of left pes of *Apatosaurus louisae*. Type. No. 3018 C. M. A., proximal view; B., lateral view; C., dorsal view; D., distal view. Ph.II., second phalanx of digit II; Ph.III., third phalanx of digit III. One-fourth natural size.

Digit IV has two phalanges. The proximal element is smaller than any of those previously described of the first row and may be distinguished from them by the fact that its longest side is external. Its principal features are clearly shown in fig. 28. The second phalanx of this toe, which is missing, is present in specimen No. 89 C. M. It is a vestigial, lozenge-shaped element having a slightly concave, thickened articular end, but is depressed anteriorly terminating in a transversely rounded obtuse border. This missing proximal phalanx of digit V is shown by

specimen No. 89 C. M. to be slightly smaller than the terminal of the fifth toe. Viewed from above it is subrectangular in outline but in other particulars resembles the terminal of digit IV. Both of these terminal bones were probably without a horny covering and may have been embedded entirely within the integument of the foot.

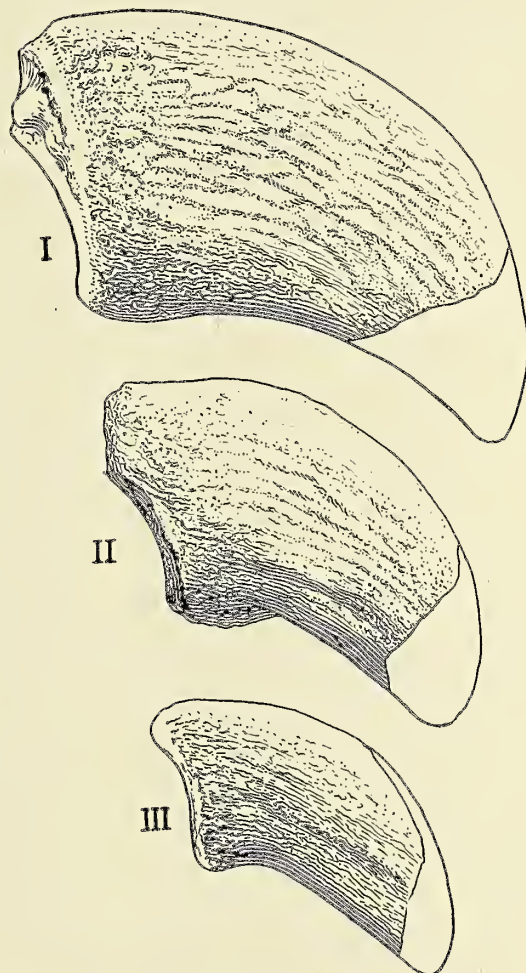


FIG. 30. Unguals of left pes of *Apatosaurus louisæ*. Type. No. 3018 C. M. Lateral views. I, II, III, unguals of digits I, II, and III respectively. One-fourth natural size.

The robustness of the elements comprising the inner side of the pes, apparently indicates that the main weight of the animal was borne by that portion of the foot. Digits IV and V were certainly undergoing atrophy as the phalanges of these outer toes are already functionally obsolete.

The principal dimensions of these various bones of the pes are given in the table of measurements below.



## COMPARATIVE MEASUREMENTS OF METATARSALS

Meta- tarsals	Greatest length		Greatest transverse diam- eter proximal end		Greatest transverse diam- eter distal end		Greatest antero-posterior diameter of proximal end	
	No. 3018 C. M.	No. 89 C. M.	No. 3018 C. M.	No. 89 C. M.	No. 3018 C. M.	No. 89 C. M.	No. 3018 C. M.	No. 89 C. M.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
I	195	145	147	95	186	136	163	135
II	213	174	172	98	149	115	185	125
III	236	188	97	83	117	94	135	97
IV	238	201	153	119	115	94	101	93
V	...	192	...	144	...	69	...	60

## COMPARATIVE MEASUREMENTS OF PHALANGES

Phalanges	Greatest Length		Greatest Breadth		Greatest Depth	
	No. 3018 C. M.	No. 89 C. M.	No. 3018 C. M.	No. 89 C. M.	No. 3018 C. M.	No. 89 C. M.
	mm.	mm.	mm.	mm.	mm.	mm.
Proximal phalanx digit I . . . . .	90	85	101	97	97	...
Proximal phalanx digit II . . . . .	101	91	119	107	95	82
Proximal phalanx digit III . . . . .	91	79	97	85	80	...
Proximal phalanx digit IV . . . . .	82	70	92	79	75	48
Proximal phalanx digit V . . . . .	...	32	...	50	...	28
Second phalanx digit I (ungual)	248e	198	99	65	158	118
Second phalanx digit II . . . . .	48	40	80	78	87	67
Second phalanx digit III . . . . .	43	75	77e	85	76e	...
Second phalanx digit IV . . . . .	...	29	...	53	...	35e
Third phalanx digit II (ungual)	234e	167	70	62	128	99
Third phalanx digit III . . . . .	...	17	...	41	...	31
Fourth phalanx digit III (ungual)	170	120	50	40	84	...

e = estimated.

## THE MOUNTED SKELETON.

The skeleton of *Apatosaurus louisæ* is one of four mounted specimens of this genus now on exhibition in as many museums of this country. Named in the chronological order of their mounting these are in the Field Museum of Natural History, Chicago, 1903; the American Museum of Natural History, New York City, 1905; Carnegie Museum, Pittsburgh, 1913; and the Peabody Museum of Natural History, New Haven, Conn., 1930. In the matter of perfectness of preservation the present specimen is even more complete than the famous *Brontosaurus excelsus* skeleton in the Peabody Museum of Natural History of New Haven. In size there is little choice between them as all are large adult animals.

The Carnegie Museum specimen has been mounted in an upright quadrupedal pose, and, standing in the exhibition hall alongside the well known *Diplodocus carnegii* skeleton of slenderer proportions, it forms an association that serves to emphasize its ponderous size and massiveness of structure, see Pl. XXXV.

The preparation and mounting of this skeleton was done under the direction of Mr. Arthur Coggeshall, assisted by Messrs. Louis Coggeshall and Albert Moorehouse. This work was accomplished in three years, a record so far as time is concerned.

The vertebral column is supported by a linear series of steel castings that closely conform to the undulating shape of the underside of the vertebræ, and these castings in turn are supported at the required height by heavy pipe standards securely anchored in the base. The sections of vertebral castings after having been placed in position were welded together to form a continuous whole. This method, first devised and used by Mr. Coggeshall in mounting the skeleton of *Diplodocus*, was much improved on the present specimen in being made much lighter in construction and in more closely adapting it to the shape of the bones. The limbs and other bones are held in position by half-round iron bars having the flat sides fitted closely to the inequalities of the bones. By these means the heavy parts of the skeleton are held in their proper articulated positions, and so skillfully has this work been done that the observer is hardly aware of the supporting framework. With the skull in position the specimen has a total length between perpendiculars of about 71 feet and 6 inches. If the missing eighteen terminal caudal vertebræ were added to the tip of the tail, in order to make it conform to known evidence, the skeleton will reach an estimated length of 76 feet, 6 inches. The highest point, at the tops of the spinous processes of the anterior sacra, is 14 feet, 8 inches, above the base.

In preparing the specimen, all missing parts of the vertebræ were restored and distortions were corrected. The three posterior cervicals, Nos. 13, 14, and 15, however, were so badly crushed out of shape that it was not deemed expedient to correct them and they have been replaced in the skeleton by replicas, and the originals in their distorted condition were placed in storage. Likewise the sixteenth caudal vertebra, so far as I could make out, is entirely restored but Mr. Louis Coggeshall assures me that core parts of the vertebral centrum are present but have been covered in restoring it to the proper form.

One of the striking features brought out by this skeleton, through the articulation of the bones, is the prolonged elevation of the anterior caudal region as it extends backward from the sacrum before beginning its drop toward the ground. In my opinion this feature would have been more emphasized had the first caudal



been fully articulated. As it stands the centrum of this caudal is farther away from the last sacral centrum at the top than at the bottom and the zygapophyses are not fully engaged. Had these bones been fully articulated the tail would have had more of an upper arcuation and this part of the animal would have been in full accord with the more recently mounted skeleton of *Diplodocus* in the United States National Museum. It is fast becoming obvious that all Sauropodous dinosaurs, when properly posed, have this lizard-like upward curve of the anterior caudal region.

Close inspection of the dorsal segment of the vertebral column clearly shows these vertebræ to have been too widely spaced thus giving undue length to the thoracic region. The scapula should also be drawn inward closer to the ribs, but with these few critical remarks, I wish to observe that the skeleton as a whole is well posed and well articulated in the light of our present knowledge of these animals.

In the mounted skeleton the fore feet were provided with restored unguals on digits II and III and a full complement of phalangials. The negative evidence drawn from several articulated Sauropod fore feet indicates a reduction in the number of phalangials and unguals and in the illustration of the skeleton, see Plate XXXIV, these extra bones have been omitted.

#### RESTORATION OF THE SKELETON

The restoration of the skeleton of *Apatosaurus louisæ*, see Plate XXXIV, is based primarily on the mounted skeleton in the Carnegie Museum. The illustration was drawn with the greatest care by Mr. Sydney Prentice, from orthographic projection drawings of each bone made separately and then assembled in the figure as a whole, after the pose of the mounted skeleton. Missing parts of bones are indicated by distinctive shading. Missing bones in a few instances have been drawn with certain modifications from the evidence furnished by other specimens of this genus. Distortions were corrected at the time of preparing the skeleton so few corrections were necessary by the draughtsman. About the only structural details of *Apatosaurus*, which may be considered unknown at the present time are the skull, lower jaws, and the successional changes and total number of the chevron bones.

As shown in previous restorations of this animal, the shortness of the thoracic region as contrasted with its other vertebral proportions is most striking. The extension of the tail into an extraordinarily attenuated "whip lash" is the outstanding contribution of the present restoration, where the tail is illustrated in its entirety for the first time.

The restoration embodies all of the latest information concerning the skeletal

structure of *Apatosaurus*, and with the exception of some slight errors of articulation due to having closely copied the position of the bones in the mounted skeleton, already commented on in previous pages, it is believed to be the most faithful presentation of the skeleton of this animal yet attempted.

The first skeletal restoration<sup>33</sup> of *Apatosaurus* (*Brontosaurus*) was made under the direction of Professor O. C. Marsh in 1883, and in most respects it was more nearly correct than his emended restoration which appeared eight years later.<sup>34</sup> Three additional posterior dorsal vertebræ, a lumbar and two cervicals, were added to the vertebral column, and the number of ribs was increased from eighteen to twenty-six. The crest of the dorsal arch was carried forward nearly to the mid-length of the thoracic region. As is now known, with the exception of the added cervicals, all of the other changes were in error. Riggs<sup>35</sup> was the first to call attention to these mistakes and in the same paper presented a third restoration based upon a partial skeleton in the Field Museum of Natural History, which for the first time showed the correct number of dorsal vertebræ.

The gradual evolution of our knowledge concerning the structure of the vertebral column in *Apatosaurus* is clearly set forth in the table below.

	Restoration No. 1 Marsh 1883	Restoration No. 2 Marsh 1891	Restoration Riggs 1903	Restoration <i>A. louisæ</i> 1934
Number of cervicals.....	11	13	13	15
Number of dorsals.....	9	13	10	10
Number of lumbar.....	1	1	0	0
Number of caudals.....	51	49	46	84

The crest of the dorsal arch stands just in front of the sacrals, as first determined by Riggs.

#### PARTIAL DESCRIPTION OF A SKELETON OF *APATOSAURUS EXCELSUS* (MARSH)

*Brontosaurus* Hatcher, J. B., Science, N.S. vol. XIV, No. 365, 1901, pp. 1015-1017; Ann. Carnegie Museum, vol. I, 1902, pp. 356-376, pls. 19-22, 14 text figs.

A second specimen of *Apatosaurus*, No. 563 C. M., furnished much supplemental information regarding the skeletal structure of this genus, and as a large number of illustrations were already prepared it was decided to include them with appropriate text in the present paper. Most of these illustrations were made more than thirty years ago by Mr. Sydney Prentice under the direction of the late Mr. J. B. Hatcher. Since the skeletal parts of *Apatosaurus louisæ* have been described

<sup>33</sup>Marsh, O. C., Amer. Jour. Sci., XXVI, 1883, Pl. I.

<sup>34</sup>Marsh, O. C., Amer. Jour. Sci., XLI, 1891, Pl. XVI.

<sup>35</sup>Riggs, E. S., Field Columb. Mus., Pub. 84, Geol. Ser. 1903, Pt. I, p. 195, Pl. LIII.



in detail it appears only necessary with the present specimen to call attention to such differences as are found to exist between homologous bones of the two species, and to describe in detail only those elements which either were not well preserved or were entirely absent in the *A. louisæ* skeleton.

Specimen No. 563 C. M., was collected by the writer in 1901 for the Carnegie Museum from the Morrison formation, about one mile south of Sheep Creek, Albany County, Wyoming. It was found about a quarter of a mile west of "Quarry D" which yielded the two skeletons, Nos. 84 and 94 C. M. of *Diplodocus carnegii*, but from thirty to forty feet lower in the formation. The specimen for the most part was found disarticulated, but isolated, there being no duplication of bones except for the presence of the small type specimen of *Elosaurus parvus*<sup>36</sup> and a few bones of *Pleurocoelus*<sup>37</sup> which came out of this same excavation. This specimen was identified by Hatcher<sup>38</sup> as pertaining to the genus *Brontosaurus* = (*Apatosaurus*), an identification verified by this more detailed study. An itemized list shows the following bones to be preserved: 9 cervical, 9 dorsal, 5 sacral and 18 caudal vertebræ, left ilium, both pubes, both ischia, many ribs; 3 chevrons, left scapula and coracoid, both humeri, both radii, both ulnæ, and complete right manus, scapho-lunar, right femur, both tibiæ, fibula and astragalus, 1 ungual and a few scattered foot bones.

*Cervical vertebræ*.—There are nine cervical vertebræ preserved, all but the two posterior ones being essentially complete. Comparison of these with the articulated series of *A. louisæ* appears to indicate that they represent an interrupted series from the third to the tenth inclusive. The remaining two are so fragmentary that a determination of their precise position in the neck is uncertain. They are tentatively regarded as being the 13th and 15th as shown in Plate XXXI.

The centra are slightly shorter than the corresponding elements of the *A. louisæ* neck and are as a whole bulkier. The capitular processes are relatively shorter and stouter than in the cervicals of *Apatosaurus louisæ*. The single spines of the third, fourth, and fifth cervicals are preserved intact; these which are missing in *A. louisæ*, show that bifurcation of the spinous processes in *Apatosaurus* begins posterior to the fifth cervical. There is no indication of a notch on the top of the spine of C 5, this end being almost squarely truncate, as shown in Plate XXXI.

The variations found in the arrangement of the laminæ and pleurocoels in the homologous vertebræ of Nos. 563 and 3018 C. M., respectively, are not much greater than is often found on opposite sides of a single vertebra.

The infrapostzygapophysial cavity in this specimen posterior to the fifth

<sup>36</sup>Peterson, O. A. and Gilmore, C. W., Ann. Carnegie Mus., vol. 1, 1902, pp. 490-499.

<sup>37</sup>Hatcher, J. B., Ann. Carnegie Mus., vol. 2, 1903, pp. 9-14.

<sup>38</sup>Hatcher, J. B., Ann. Carnegie Mus., vol. 1, 1902, Pt. XIII, p. 356.

vertebra is consistently subdivided by an oblique accessory lamina which connects the infrapostdiapophysial with the horizontal lamina, whereas in the cervicals of *A. louisæ* this cavity remains undivided throughout the series. The median notch at the base of the metapophyses is usually wider in the cervicals of *A. louisæ*. The measurements of these vertebræ will be found in the table of comparative measurements on page 196.

*Dorsal vertebræ*.—Nine dorsal vertebræ are preserved with specimen No. 563 C. M., six of which lack their spinous processes. These vertebræ, although found disarticulated, are regarded as forming a continuous series from the first to the ninth inclusive. Comparison with the dorsal series of *A. louisæ* shows some decided differences in their structural details and if these features can be relied upon as being constant, they furnish characters indicating their specific distinction. The constancy of these features, however, can only be determined by a comparison of a greater number of individual specimens than have been available to me.

The most conspicuous differences are found in the centra, pleurocentral cavities, neural spines, and placement of the capitular facets and hyposphene. The various lamina also show considerable variation in the two series, but since the lamina are often unlike on the opposite sides of a single vertebra, the variations found are not considered as important as those differences observed in the other vertebral structures previously mentioned.

The centra of D 1, D 2, and D 3, are strongly opisthocœlus. D 1, as in the Field Museum specimen, has the longest centrum of the dorsal series. In the type of *A. louisæ* it is shorter than D 2. The pleurocentral cavities of the anterior dorsals are quite different in the two specimens. In D 1, of *A. louisæ*, the pleurocentral cavity is the smallest of the entire dorsal series and situated at mid-height and on the posterior half of the centrum. In D 1, of No. 563 C. M., this cavity is large, situated at mid-height but about equally spaced between the two ends of the centrum. In D 2, the cavity is reduced in size but located similar to D 1. D 3 has the smallest pleurocentral cavity of the series, situated slightly above the mid-height of the centrum. In *A. louisæ* these cavities increase in size from D 1 to D 3, accompanied by a progressive elevation upward on the side of the centrum. Throughout the rest of the dorsal series the pleurocentral cavities are subequal in size and similarly located near the top of the centra. Centrally placed antero-posteriorly, from D 4, posteriorly they move forward in the posterior members of the series, and are closer to the anterior than to the posterior end.

The neural spines or metapophyses on the anterior dorsals vary somewhat in the depth of the median division of the spines in homologous vertebra of the two specimens, being relatively deeper in specimen No. 563 C. M. In this speci-



men the bottoms of these notches are narrow whereas in the *A. louisæ* vertebræ they are widely U-shaped. Compare Pls. XXV and XXXII. That this narrowness of the bottom of the notch separating the metapophyses is not a constant character in *A. excelsus* is indicated in the Field Museum specimen by wide notches on D 3 and D 4.

The capitular facets, on D 1 of No. 563 C. M., are situated anterior to the pleurocentral cavity and slightly below the mid-height of the centrum; on D 2, they are much enlarged vertically but occupy practically the same position; on D 3, they are still on the sides of the centrum but near the top; on D 4, they have shifted to a position above the mid-height of the neural arch. These changes in position of the capitular facets in the anterior dorsals are in accord with the conditions found in the type of *A. (Brontosaurus) excelsus*, and in the Field Museum specimen of *Apatosaurus*. In *A. louisæ*, however, these facets are on the sides of the centra in D 1, and D 2, but in D 3, the facet is high on the arch as in D 4, of specimen No. 563 C. M.

Corresponding with this delayed upward shifting of the capitular facets, it is found that the hyposphene-hypantrum articulation first appears on D 4, whereas in *A. louisæ* it first occurs in D 3. In specimen No. 563 C. M., the hyposphene reaches its strongest development on D 6, but gradually diminishes in size posteriorly so that on D 9 it persists as scarcely more than a thin vertical bar of little or no function. Throughout, the dorsals having this type of articulation are more robustly developed than the corresponding elements of the *A. louisæ* skeleton. In the Field Museum specimen, Riggs<sup>39</sup> notes that the hyposphene reaches its strongest development on D 4 as in *A. louisæ*. In No. 563 C. M., within the area of strongest development the hyposphene is supported from below by a pair of strong buttresses that arise from the arch on a level with the top of the neural canal. Similar buttresses are present in the Field Museum specimen but are entirely absent on the dorsals of *A. louisæ*.

The centra of the posterior dorsals are subelliptical in outline, the transverse diameter considerably exceeding the vertical, whereas the same dorsals in the *A. louisæ* skeleton have these diameters subequal. The transverse processes throughout the dorsal series are more robustly developed, see Pl. XXXII, than in *A. louisæ*, the most pronounced difference in this respect being found in D 3. Comparison of these two series of dorsals shows that the dorsals of *A. excelsus* are stouter, more compact, and more fully braced by supporting lamina, than in *A. louisæ*.

*Sacral vertebræ*.—In specimen No. 563 C. M., the sacrum is composed of five vertebræ coalesced by their centra. The primary sacrum in the Sauropoda consists

<sup>39</sup>Riggs, E. S., Field Columb. Mus., Pub. No. 82, Geol. Ser., No. 4, 1903, p. 175.

of three vertebrae to which has been added a posterior dorsal (sacro-dorsal) and an anterior caudal (sacrocaudal), but in the present description all will be referred to as sacrals.

In addition to the coalescence of the vertebral centra their union is further strengthened by the coössification of their zygapophyses, neural arches, and bases of their diapophyses. In this specimen the spines of S 2 and S 3 are fused for their entire length, but in the type of the species and in the Field Museum specimen, both slightly larger individuals, the spines of S 2, S 3, and S 4, are thus co-joined. In the type of *A. minimus* (No. 675 A.M.N.H.)<sup>40</sup> however, the spine of S 5 is also coössified with the others. Thus in *Apatosaurus* there are from two to four spines coalesced in the sacrum. Although the evidence at hand may indicate this feature to be a specific difference, I am inclined to the opinion that it will not prove to be constant, varying with and perhaps influenced by the age of the individual.

At least eight sacra of *Apatosaurus* are now available for comparison and these apparently show, as first pointed out by Riggs,<sup>41</sup> that the number of coalesced sacrals is largely determined by the age of the individual. In *Apatosaurus* it now seems definitely established that the normal number is five co-joined vertebrae, although an occasional individual may show an additional dorsal or caudal thus coössified.

The neural spines decrease regularly in height from front to back. The spine of S 4 is entirely missing in this specimen but that it stood free as those of S 1 and S 5 is indicated by the absence of a sutural surface on the posterior border of the spine of S 3. Supradiapophysial laminae give lateral support to the spines, those of S 2 being especially robust in character. The transverse axis of the sacrum passes through S 3, and it is of interest to observe that the diapophysial processes are so arranged as to brace and strengthen this portion of the skeleton against the fore and aft stresses placed upon it. Reference is made to the divergent ray-like arrangement of the diapophysial processes when viewed from above, see figs. 31 and 36. The processes of S 1 and S 2 are directed forward and outward, and those of S 3, S 4, and S 5, are directed backward and outward. In the present articulated condition it is impossible to properly study the structural arrangement of the sacral ribs and their attachments and on that account their description is omitted.

Sacral five as shown in fig. 31 is attached to ilia by broad transverse processes but no trace of its division into diapophysis and sacral rib is to be observed.

The height of the postzygapophyses, see fig. 31, which looks almost directly downward, above the level of the neural canal in S 5 would seem to indicate that the caudal identified as C 1 might be C 2 and that the first is missing in this speci-

<sup>40</sup>Mook, C. C., Bull. Amer. Mus. Nat. Hist., XXXVII, 1917, fig. 1c.

<sup>41</sup>Riggs, E. S., Field Columb. Mus., Pub. No. 82, Geol. Ser., 1903, p. 182.



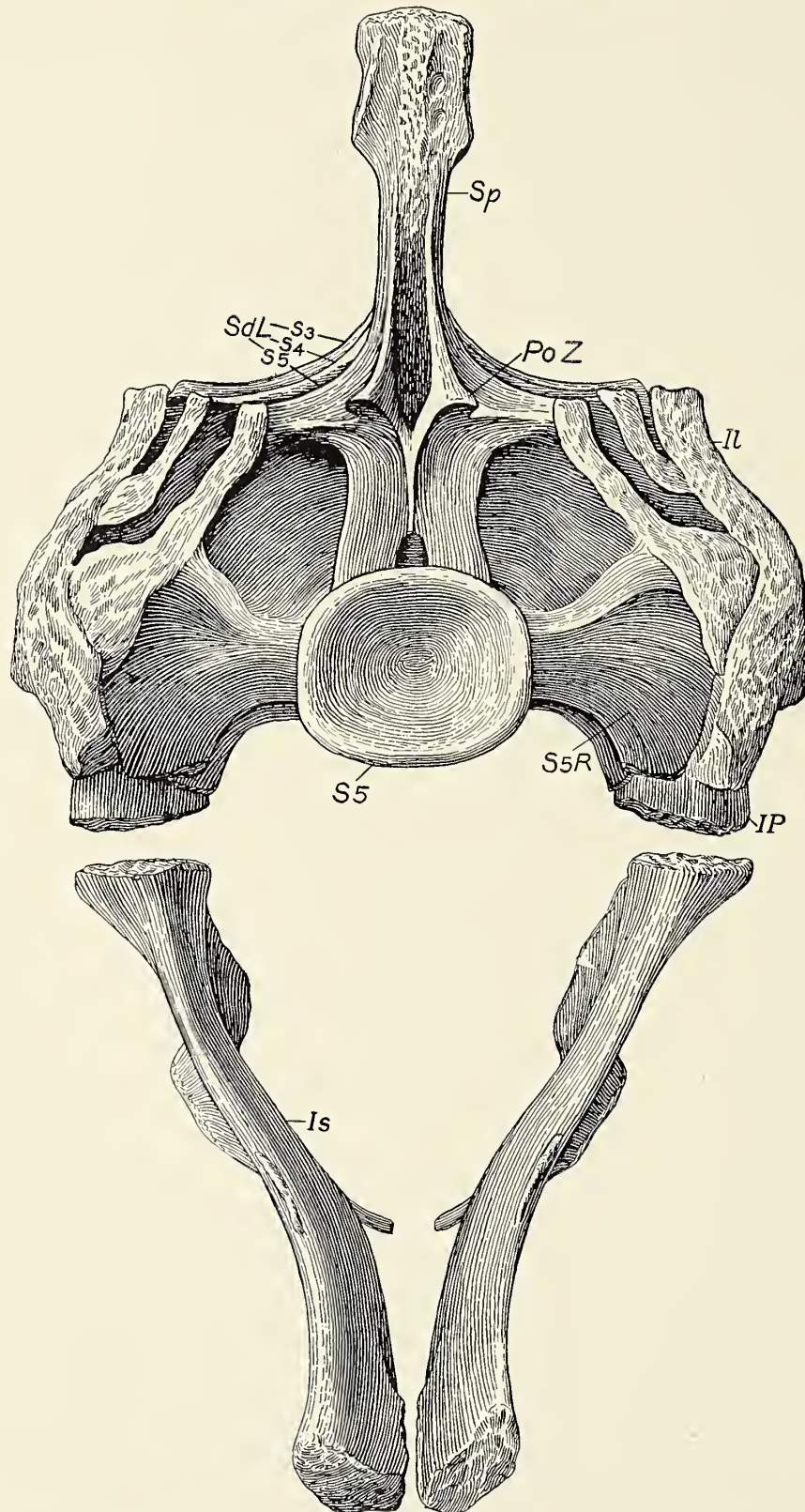


FIG. 31. Pelvis and sacrum of *Apatosaurus excelsus* No. 563 C. M. Posterior view. *Sd L.* 3, 4, 5, supradiapophysial laminae of sacra 3, 4, and 5 respectively; *il.*, ilium; *i.p.*, ischiac peduncle; *is.*, ischium; *po.z.*, postzygapophyses; *s 5.*, sacral five; *s 5R.*, fifth sacral rib; *sp.*, spine of fifth sacral. Right ilium restored from the left side. One-tenth natural size.

men. The zygapophyses are braced from above by the strong suprapostzygapophysial laminæ which merge into the posterior face of the spine above its mid-height. The principal features of the posterior view of S 5 are well shown in fig. 31.

The sacriocostal yoke is formed by the coalesced distal rib articulations of the first four sacrals, to which the lower part of the transverse process of S 5 is also attached. The inferior surface of this yoke contributes to the formation of the acetabulum. These ribs unite with nearly the whole length of the sacral centra as in the type of *A. excelsus*.

#### MEASUREMENTS OF SACRAL VERTEBRÆ

Greatest length of five coössified centra.....	1183 mm.
Height of coalesced spines.....	543 mm.
Fore and aft diameter of two coalesced spines at summit.....	303 mm.
Greatest height over all of S 1.....	1085 mm.
Greatest height over all of S 5.....	980 mm.
Greatest expanse of transverse processes of S 5.....	804 mm.

*Caudal vertebræ*.—Eighteen caudal vertebræ are preserved with specimen No. 563 C. M. All of these were found disarticulated, but by comparison with the articulated caudal vertebræ of *A. louisæ* they have been allocated in series as shown in Plate XXXIII. Eleven of the eighteen elements have transverse processes, thus indicating their anterior position in the tail. Study of their principal dimensions, as shown in the table of measurements p. 210, seems to indicate that they represent a continuous series from the first to the ninth inclusive. In the type of *A. excelsus*, as in the Field Museum *Apatosaurus*, twelve of the caudals bear transverse processes. The American Museum specimen has but eleven, whereas the type of *A. louisæ*, and No. 3378 C. M. both show fourteen. From this evidence it is quite apparent, that any mistake made in the allocation of these scattered elements, cannot be very seriously in error. The remaining nine, however, cannot be so certainly placed and their allocation should be considered tentative.

Viewed from the end the centra of these anterior vertebræ are all subequal in transverse and vertical diameters, in this respect differing from the anterior caudals of *A. louisæ* which has the vertical exceeding the transverse diameter. The lengths of the centra are relatively shorter, and there is no indication of a ball on the posterior end of C 1, and it is only slightly indicated on C 2, and C 3.

The first and third caudal vertebrae of this specimen are completely preserved and these apparently indicate that there is a more rapid shortening posteriorly of the spinous processes than has been indicated in the restoration of the missing spine tops in the mounted skeleton of *A. louisæ*, consequently in this respect the present restoration, plate XXXIV, is probably slightly in error.



The first caudal in *Apatosaurus* has a number of characteristics which distinguish it from the other vertebræ of the caudal series. The most outstanding is the great plate-like development of the transverse processes. These spring from the sides of the upper half of the centrum and the neural arch, and extend directly outward on a level with the postzygapophyses terminating in a slightly expanded end that is nearly vertical in this specimen. These processes rapidly decrease in vertical extent posteriorly, and posterior to C 1, have their outer ends beveled off from above downwards. In the first three caudals these processes are perforated by a large foramen-like opening on either side of the neural arch.

In C 3, however, these perforations do not pass entirely through the bone. Practically similar conditions obtain in the type of *A. excelsus*. That these foramina are not always present in individuals of this species is shown by their absence<sup>42</sup> in C 1, of the Field Museum specimen. They are not present in any of the caudals of *A. louisæ*. Holland has used this feature as one of the characteristics for distinguishing *A. excelsus* from *A. louisæ* but in view of their variable character, it would seem not to be of importance in that connection.

*Cervical ribs.*—Cervical ribs are present on all of the vertebræ and except the fifteenth pair all are anchylosed by their tubercular processes to the diapophyses, and by their capitular processes to the parapophyses. The fifteenth pair are to be recognized by their non-coalescence with the vertebra, see pl. XXXI, their short fore and aft diameter and broadly curved border between the tubercular and capitular processes. In most of the cervicals the tubercular process extends downward and slightly outward from the diapophysis and thus increases the width of the vertebra. The ribs have anterior and posterior branches that usually parallel the centrum, but in none of those present does the rib exceed the centrum in length. These ribs differ from those of *A. louisæ* in having a blunt extension that projects forward of the line of the tubercular process, whereas in *A. louisæ*, this end is smoothly rounded but with a heavy node-like projection that projects downward and outward.

*Scapula and coracoid.*—The left scapula with a portion of the coössified coracoid is present in this specimen, as shown in fig. 32. In so far as it can be compared with the complete scapula of the type of *A. excelsus*, the two bones are in the closest accord, compare fig. 32 with C, fig. 10. From the scapula of *A. louisæ* this bone may be distinguished by the backward inclination of the posterior border near the distal end, by the right-angled trend of the transverse ridge or spine and the increased area of the muscular fossa above this ridge. On account of the close resemblances to the typical *A. excelsus* scapula it is presumed that the missing

<sup>42</sup>loc. cit., Pl. XLVI, fig. XII.

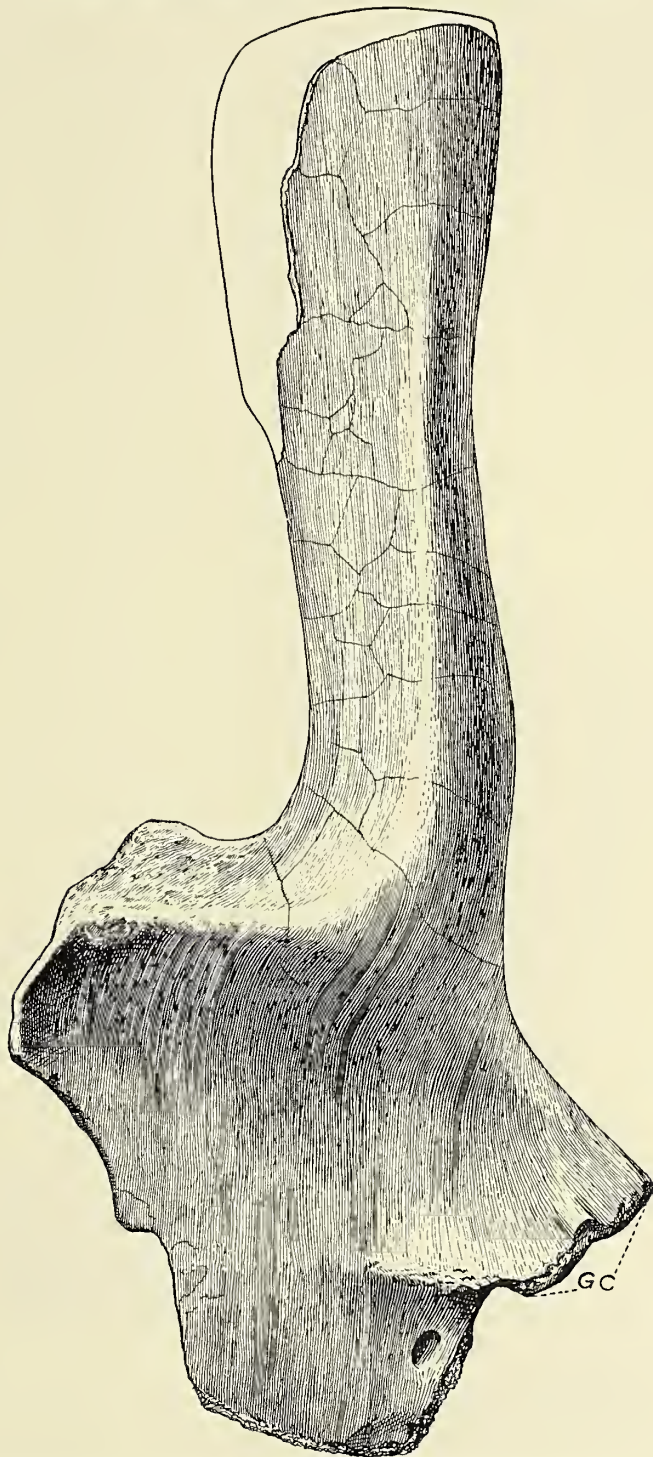


FIG. 32. Left scapula and portion of coracoid of *Apatosaurus excelsus*, No. 563 C. M. Lateral view. G.C., glenoid border. One-tenth natural size.

anterior border of the upper portion of the blade had a forward expansion and it has been thus restored. The measurements of this bone will be found on page 216.

The coracoid is too incomplete to offer any basis of comparison.



"*Humerus*.—<sup>43</sup>The shaft of this bone is much constricted, while the extremities are greatly expanded transversely, the proximal to a much greater extent than the distal. There is a very prominent deltoid ridge extending along the anterior external border from the proximal and throughout one-half the length of the bone. Between the ridge and the inner margin there is on the anterior surface a rather deep basin, subtriangular in outline, bounded above by the anterior border of the slightly thickened broad proximal end and externally and internally by the deltoid ridge and internal lateral margins, which converge inferiorly where the shaft becomes much restricted. The proximal end has the transverse diameter much expanded while the fore and aft is quite short. In the present specimen the differences between these two diameters is somewhat magnified through distortion due to crushing. Superiorly the proximal end is regularly convex, so that when seen

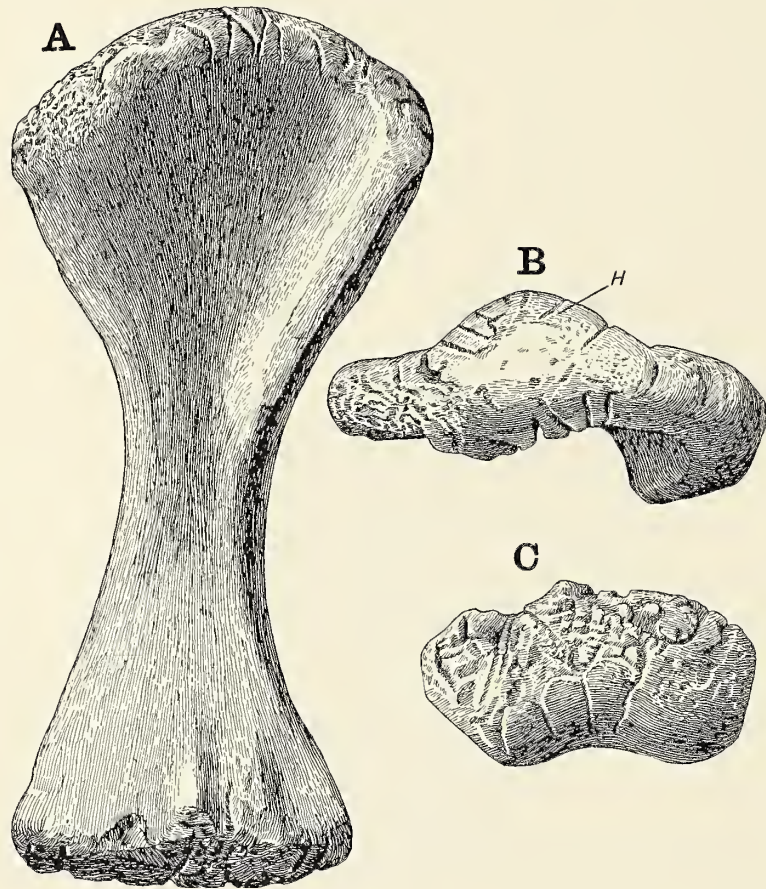


FIG. 33. Right humerus of *Apatosaurus excelsus*, No. 563 C. M. A., front view; B., proximal end; C., distal end; H., head. One-tenth natural size. (New figures)

<sup>43</sup>The right fore limb and foot of specimen No. 563 C. M. has been described in detail by Hatcher (Annals Carnegie Museum, I, 1902, pp. 360-373) and with the exception of some omissions of references to figures and plates and tables of measurements) the description is repeated here in its entirety.

from behind or in front its upper border describes an almost perfect arc, the chord of which in the present specimen has a length of 600 mm. The head is placed about midway between the external and internal borders, but a little nearer to the latter, and is directed rather strongly backward much as in the Testudinata. It is very rugose, only moderately expanded in either direction."

"Distally the transverse diameter of the humerus is about double the fore and aft. The articular surface is exceedingly rugose and deeply pitted as though covered in life with heavy cartilaginous epiphyses which never became thoroughly ossified and through the intermedium of which it articulated with the radius and ulna. On the posterior border there is an emargination indicative of an anconeal fossa. This is extended into the articular area in such manner as to cause a slight median constriction on the posterior side directly opposite a slight anterior expansion on the anterior surface. There is a small and imperfectly defined external condyle. The posterior border of the humerus is regularly convex transversely throughout most of its length, though much flattened proximally and slightly grooved distally."

"*The Radius and Ulna.*—These bones are subequal in size. The distal third of the ulna is a little more slender than the same portion of the radius. The shaft of the radius is constricted medially while the ends are about equally expanded. The proximal end is semi-circular in cross-section, the convex surface fitting nicely into the radial groove on the anterior surface of the proximal end of the ulna. Proximally the radius articulates only with the anterior and internal portion of the distal articular surface of the humerus. The proximal end of the ulna entirely encloses that of the radius posteriorly and externally so that its articular surface is opposed to that of the distal end of the humerus posteriorly throughout its entire breadth, while at the same time presenting a broad and deep articular surface on the anterior projection which encloses the radius externally for contact with that of the anterior and external surface of the humerus. The contact of the radius with the humerus is thus limited to the antero-internal surface of the humerus instead of the antero-external as determined by Osborn and Granger,<sup>44</sup> so that these bones are not so completely crossed as these authors had supposed, but occupy positions almost identical with those figured by the late Professor Marsh as obtaining in the fore limb of *Morosaurus*.<sup>45</sup> Seen from above the proximal end of the ulna may best be described as tri-radiate. The rays are formed by the posterior anconeal spine, the directly opposite external anterior projection and the widely expanded internal portion. The first two of these are subequal and much smaller than the last. All are separated by concave surfaces. There is a deep cavity on the posterior

<sup>44</sup>Bull. Am. Mus. Nat. Hist., vol. XIV, pp. 199-208.

<sup>45</sup>Part I, Sixteenth Ann. Report U. S. Geol. Survey, pp. 143, 244, Plate XXXVII.



surface between the anconeal spine and the internal, lateral margin of the ulna. Distally the radius shows a prominent rugosity on the posterior side near the external border. This commences about four inches from the distal extremity and continues as a prominent narrow ridge for a distance of nine inches. At about one-third the distance from the lower to the upper end of this rugosity it is interrupted by a deep groove which starts on the inner side, runs obliquely downward and outward, completely bisecting the rugosity. This groove doubtless served for

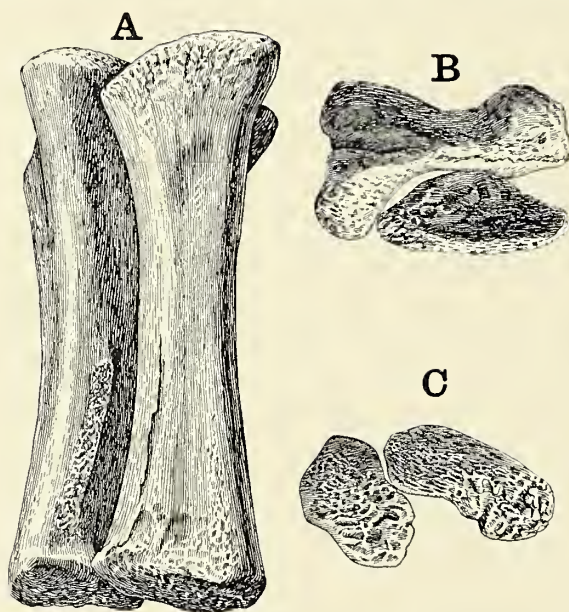


FIG. 34. Right radius and ulna, articulated, of *Apatosaurus excelsus*. No. 563 C. M. A., front view; B., view of proximal ends; C., view of distal ends. One-tenth natural size. (New figures)

the transmission of an artery. Opposed to this rugosity on the radius there is a similar one on the middle of the internal surface of the ulna near its distal extremity. These rugosities doubtless served for the attachment of the muscles which held these bones in place. Seen from below, the articular surface of the distal end of the radius has the form of an elongated ellipse with an area somewhat exceeding that of the distal end of the ulna, which takes the form of an oblique quadrangle with its two axes nearly equal. There is, on the internal surface of the distal end of the ulna, a rather deep emargination or fossa for the reception of the rounded postero-external angle of the distal end of the radius. This emargination appears, though less distinctly, on the internal border of the distal articular surface of the ulna. Its presence affords great assistance in the proper adjustment of these bones, since, when they are so placed that the convex surface of the proximal end of the radius fits nicely into the radial groove of the ulna and the postero-external angle of the distal end of the radius in this fossa, there can be no question as to the

correct relative positions of these bones. The articular surfaces of the distal ends of the radius and ulna display different degrees of rugosity. The postero-internal portions of each are extremely rugose and deeply pitted, while toward the center the surfaces become less indented and the external half of each presents a polished surface marked with shallow corrugations."

"*The Carpus.*—There was but one carpal bone found with the present limb and foot. This agrees very closely with the description given by Osborn and Granger of the supposed scapho-lunar in *Diplodocus*, and with those authors I agree in making it homologous with that element in the mammalian carpus. If my interpretation of the position of this bone in the manus is correct the following description of this element would apply. The general form is that of a circular disc, thin in front but considerably thickened posteriorly. The superior surface is crossed antero-posteriorly by a low, broad ridge which divides it into two slightly concave and subequal surfaces, the larger and smoother of which was for articulation with the external half of the distal end of the radius, while the smaller and more rugose

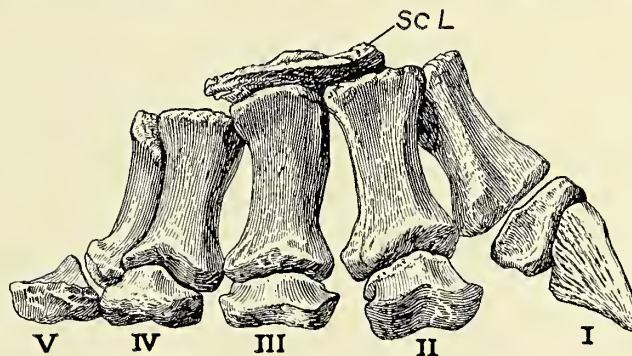


FIG. 35. Right fore-foot of *Apatosaurus excelsus*, No. 563 C. M. Viewed from the front. *ScL.*, scapho-lunar; I, II, III, IV, V, digits one to five respectively. About one-ninth natural size. (New figure)

surface articulated with the internal portion of the distal articular surface of the ulna. Inferiorly this bone presents a gentle convex, polished, but corrugated surface for articulation with metacarpals II, III, and IV. No other carpals were found with or near this foot, and after a careful study of it and the articular surfaces of the distal ends of the radius and ulna and considering the position in which metacarpals II, III, and IV lay with reference to these bones and metacarpals I and V, it appears quite probable that it was the only ossified element present in the carpus of *Brontosaurus* and therefore that the *Brontosaurus* carpus, like the tarsus, consisted of a single element."

"*The Metacarpals.*—All the elements of the metacarpus were present and in approximately their normal positions when the foot was uncovered."

"Metacarpal I is short and much the strongest bone of the entire series. The



proximal end is very deep, but much compressed. The articular surface is gently concave vertically and convex transversely. The internal lateral margin of the proximal end is regularly convex so that this margin and the proximal articular surface as well conform to the internal margin and internal articular surface of the radius with which during the life of the animal it probably had a direct, cartilaginous articulation. The external lateral margin of the proximal end is regularly concave and just in front of the articular surface there is a deep cavity for the reception of a corresponding prominence on the internal margin of metacarpal II. The external surface is rugose throughout the entire length of the bone; it is much constricted vertically in the middle, but with decided distal and proximal expansion for contact with metacarpal II. The internal lateral surface is regularly but gently convex vertically throughout the entire length of the bone and only slightly constricted vertically in the middle region. The superior surface gradually broadens from the proximal to the distal end. The inferior surface is deeply concave longitudinally, broad at the distal extremity, but reduced to a sharp narrow ridge at the proximal end. The distal articular surface has the vertical and transverse diameters subequal. It is continued well back on the palmar side of the bone in order to accommodate the thin sheet of bone which projects posteriorly from the palmar side of its proximal phalanx. There is a vertical, median groove for the accommodation of the low median keel of the latter."

"Metacarpal II is longer and more slender than the preceding, although decidedly stronger than metacarpal III. It is somewhat constricted medially both in its vertical and lateral diameters. Compared with metacarpal I it is broad, but greatly depressed. The superior as well as the distal portions of the lateral surfaces are smooth, while the inferior and proximal portions of the lateral surfaces are covered with rugosities. The inferior internal angle of the proximal end of this bone is especially modified as so to fit nicely into the deep cavity just described as present on the external lateral surface of metacarpal I. These bones are so interlocked that when placed in position a considerable portion of the proximal end of mc. II is covered over by the superior border of the cavity in mc. I, while the proximal end of the latter is raised above that of mc. II, so as to articulate directly with the radius. There is a broad, shallow excavation on the external lateral surface at the proximal end of mc. II for the reception of the internal proximal angle of mc. III. The proximal articular surface of mc. II is broad above and somewhat narrowed inferiorly. Its superior and inferior margins are bounded by nearly straight, horizontal lines. The surface is very slightly and regularly convex in all directions. The distal articular surface is broad and deep, though in the present specimen the latter diameter has been somewhat diminished by pressure.

Just anterior to the rugosity on the internal lateral surface of the proximal end of this bone there is a deep groove leading obliquely downward and forward to the palmar surface. This may have served for the transmission of a flexor tendon."

"Metacarpal III is of equal length, but decidedly more slender than mc. II. The superior surface is smooth and regularly convex. There is a noticeable lateral constriction at about the middle of the distal half of the bone. On the internal lateral surface of the proximal end there is a flat rugose area, broad proximally, but narrowed distally, which disappears toward the middle of the shaft. The internal, proximal, lateral angle is so shaped as to fit nicely into the cavity on the external lateral surface of the proximal end of mc. II, causing an interlocking of the proximal ends of these bones. The proximal articular surface is subtriangular in outline through the external superior lateral angle of the proximal end being produced into a strong triangular process which overlies a corresponding projection on the internal inferior lateral angle of mc. IV. The external outer margin on this process on mc. III presents a rounded articular surface which fits into a deep groove on the superior internal surface of mc. IV, thus causing these bones to interlock at their proximal ends, though somewhat less perfectly than mcs. I and II, and II and III. The palmar surface of mc. III is rugose and there is a broad median ridge continued throughout the entire length of the bone. The distal end is broad and deep, convex, and with an indistinct groove inferiorly."

"Metacarpal IV is shorter and more slender than mc. III. It is greatly constricted medially and at the point of greatest constriction it is nearly circular in cross-section instead of flat as in mcs. II and III. On the internal lateral surface of the proximal end there is the deep groove mentioned above for the accommodation of a corresponding prominence on the external lateral surface of mc. III. The proximal articular surface is triangular. The lines bounding the internal and superior borders are of equal length and meet at right angles so as to form the base and perpendicular of a right-angled triangle, while the hypotenuse is formed by the line bounding the external lateral border. The latter, when this bone is placed in its natural position, runs obliquely downward and inward toward the median axis of the foot. There is a broad, shallow emargination on the external lateral surface near the proximal end. The distal end presents a broad and deep articular surface concave transversely and convex supero-inferiorly."

"Metacarpal V is shorter and stronger than mc. IV. It has something of the general shape of mc. I, though not nearly so massive as that bone. It is compressed proximally, but expands distally. There is a broad, rugose, concave surface on the internal side of the proximal end. The proximal articular surface is crescentic in outline with the upper arm heavier than the lower. There is a deep constriction



on the inferior side and another less pronounced on the superior just behind the distal end. The distal articular surface is faintly convex and subcircular in outline."

"The manner in which the different elements of the metacarpus interlock at their proximal ends is suggestive of that which obtains in the mammalia and is well calculated to give stability to the manus when supporting the weight of the ponderous body. It will also, now that the position of each is definitely known, furnish important aid in assigning the various metacarpals when found disassociated to their proper positions."

"*The Phalanges*.—The entire series of proximal phalanges are present as is also the second or terminal phalanx of the first digit."

"The proximal phalanx of the first digit is longer on the external than on the internal side, so that when in position between the ungual and mc. I it appears wedge shaped, with the wedge directed toward the opposite foot. The internal lateral surface is convex and the external deeply concave. The palmar surface is produced posteriorly into a thin sheet which lies under the distal end of mc. I. The proximal articular surface is concave supero-inferiorly and there is a low, broad keel for articulation with the groove in the distal articular surface of mc. I. The distal articular surface is regularly convex supero-interiorly and concave transversely."

"The ungual of the first digit is compressed laterally but deep posteriorly. The internal lateral surface is convex, the external flat. The proximal articular surface has been so much distorted by pressure, due to the position in which it lay when imbedded, that its characters are obscured in the present specimen. The distal extremity is pointed and the entire external surface throughout the distal two-thirds of its length bears evidence of its having borne a powerful claw during the life of the individual."

"The proximal phalanx of the second digit is much the largest of the entire series. The proximal articular surface is flat and circular in outline, the vertical and lateral diameter of this end of the bone being equal. Distally this phalanx is much depressed and greatly expanded transversely. The distal articular surface is very broad but shallow and divided by a deep, median, vertical groove into two subequal lateral moieties with smooth convexly rounded surfaces. This phalanx, as well as its metacarpal, has been erroneously considered as belonging to the third instead of the second digit of the series by Professor Osborn, as will readily appear by a reference to fig. 7 of that author's paper on the 'Fore and Hind Limbs of Carnivorous and Herbivorous Dinosaurs,' published as Article XI of Vol. XII of the 'Bulletin of the American Museum of Natural History.'"

"The proximal phalanx of the third digit is short, very much depressed, more especially at the distal end, and expanded laterally. The proximal articular surface is elliptical in outline, slightly concave, with its transverse diameter about double that of the vertical. The distal articular surface is broad, but extremely shallow. There is a broad but very shallow depression in the middle, faintly dividing it into two ill-defined articular areas. The bone is of about equal transverse dimensions throughout its length."

"The proximal phalanx of the fourth digit is short and stout, much narrower than that of the third, but not so depressed. Seen from above it appears somewhat wedge-shaped, the length of the external lateral border greatly exceeds that of the internal. The proximal articular surface is slightly concave and semicircular in outline. The distal end is depressed, with an ill-defined articular surface crossed by a shallow, median vertical groove."

"The proximal phalanx of the fifth digit is more massive than that of either the third or fourth, but smaller than the corresponding bones of digits one and two. Seen from above, it presents a broadly wedge-shaped superior surface with an extended external lateral margin, while the inner margin is reduced to a sharp ridge where the proximal and distal surfaces converge and meet at an acute angle. The bone is broader and less depressed than either of the two elements last described. The proximal articular surface is irregularly quadrangular in outline, the transverse dimension about double the vertical. Distally there is a poorly defined articular surface."

The principal dimensions of the phalanges found with this limb and manus are given in the table, page 226.

"*The Sesamoids*.—A small, oblong rounded sesamoid was found in position on the palmar side, lying between the distal end of mc. III and its proximal phalanx. There is little doubt that digits II and IV at least bore similar sesamoids in the same position, while others may have been interposed between some of the phalanges. It is not at all impossible that the small ossicles mentioned by Osborn and Granger as found associated with other elements of the manus of *Diplodocus* and referred by those authors to the carpus were in reality phalangeal sesamoids, as is evidently the case with the present ossicle. The maximum lateral dimension of this bone is 60 mm., vertical 26 mm., while the fore and aft diameter exactly equals the vertical."

#### PELVIS

The pelvis is represented by the left ilium, left pubis and both ischia. All of these bones are uncrushed and in excellent preservation.



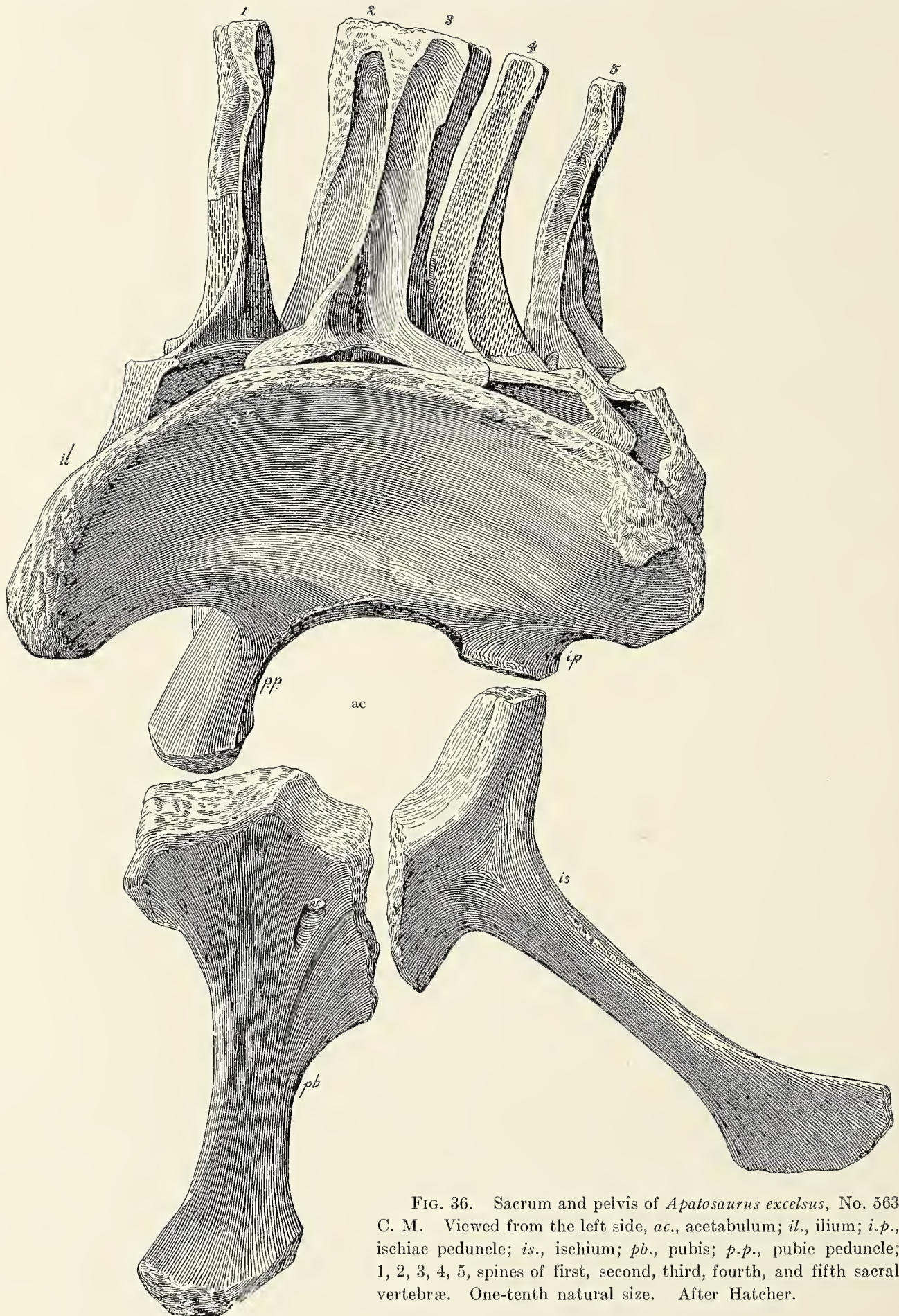


FIG. 36. Sacrum and pelvis of *Apatosaurus excelsus*, No. 563 C. M. Viewed from the left side, *ac.*, acetabulum; *il.*, ilium; *i.p.*, ischiac peduncle; *is.*, ischium; *pb.*, pubis; *p.p.*, pubic peduncle; 1, 2, 3, 4, 5, spines of first, second, third, fourth, and fifth sacral vertebrae. One-tenth natural size. After Hatcher.



*Ilium*.—The left ilium was found articulated with the sacral vertebræ as shown in fig. 36, and its relationships to the sacrum may be regarded as perfectly normal, since there is no evidence of distortion or displacement. If this assumption is correct, it is in perfect agreement with the Field Museum specimen, in showing the tops of the diapophysial processes above the top border of the ilium, and with having the sacral centra almost entirely hidden by it in a lateral view.

The ilium is produced far in front of the pubic peduncle into a gradually narrowing blade that turns slightly outward and decidedly downward. The lower border of this blade forms an acute angle with the anterior border of the pubic peduncle, as in the Field Museum specimen. In this respect both specimens are quite unlike the nearly right-angled notch found in the ilia of the types of *A. louisæ* and *A. excelsus*.

The pubic peduncle is relatively shorter than in *A. louisæ*, although in all other respects the two bones are very similar.

*Pubis*.—The pubis is elongate, with massive expanded ends, especially the proximal. The acetabular surface is broad as is the articular surface for the pubic peduncle of the ilium. That there was a tendency, in this specimen, for the pubis to coössify with the peduncle is evidenced by the upward extension of the lateral

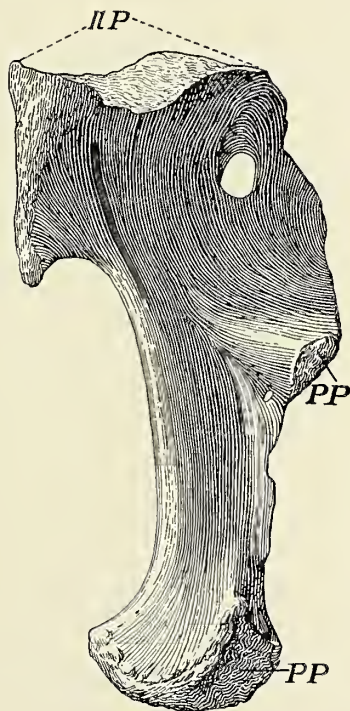


FIG. 37. Left (reversed) pubis of *Apatosaurus excelsus*, No. 563 C. M. Internal view. *il.p.*, articular surface for pubic peduncle; *p.p.*, articulating surfaces for union with opposite pubis. One-tenth natural size.



surfaces of the pubis as shown in fig. 37. A pelvis of *Diplodocus*, No. 94 C. M., shows a similar but more exaggerated condition.

Posteriorly the pubis unites by its thinned margin with the ischium and in this specimen, unlike the *A. louisæ* type, there is no indication of coössification. The posterior margin, below the ischiac border, curves strongly inward and the center presents a thickened ovate rugose surface for union with the pubis of the opposite side. On the inner side of the distal end is a larger rugose surface that, with the one described above, forms the main part of contact between the two pubes on the medial line. It seems quite probable that this union was a cartilaginous one, since in none of the available specimens is there evidence of coössification. Between these two contact points the inner border presents a thin, sharp edge. When the pubes are articulated these intermediate borders are not in contact but leave a narrow slot-like interval between. The distal end presents a roughened surface that may have been capped with cartilage. The pubic foramen is entirely closed in by bone and, viewed from the outer side, passes upward through the bone immediately below the anterior acetabular border.

*Ischium*.—The ischia are more elongate than the pubes. The proximal end is widely expanded with articulating surfaces for union with the pubis and the ischiac peduncle of the ilium is shown in fig. 36. The proximal end between these articulations forms the postero-inferior boundary of the acetabulum. The shaft is relatively slender and toward the expanded distal end the bone is trihedral in cross-section. When articulated, see fig. 31, the ischia curve strongly inward to meet on the median line. In *A. louisæ*, where they are coössified, the ischia meet for half their length. In this specimen, however, their junction would be somewhat shorter, as these ischia give no evidence of coalescence. If fully articulated the two bones would form a shallow trough on the upper side, and a broadly rounded inferior surface.

The principal feature of this bone is clearly shown in figs. 31 and 36. Their dimensions are given on page 229.

#### DISCUSSION OF THE GENUS *APATOSAURUS*

The genus *Apatosaurus* was proposed by Professor O. C. Marsh in December 1877, when he briefly described *Apatosaurus ajax*,<sup>46</sup> the genotype, based upon a considerable portion of a skeleton. In this same paper the species *A. grandis* was also briefly described. Two years later the genus was further characterized, largely on the narrowness of the blade of the scapula, the quadrangular shape of

<sup>46</sup>Marsh, O. C., Amer. Jour. Sci., 3d ser., XIV, 1877, p. 514.

the coracoid, and the presence of three coössified vertebræ in the sacrum. All of these bones were illustrated.<sup>47</sup> In this same paper a third species *A. laticollis* was named. In 1915 Holland added a fourth species, *A. louisæ*, based on the skeleton here described.

In 1917 Mook named a fifth species, *A. minimus*, based on a sacrum with attached ilia.

In 1903, Riggs<sup>48</sup> in order to identify a specimen secured by him and now mounted in the Field Museum of Natural History, Chicago, made a study and comparison of the types of *Apatosaurus* and *Brontosaurus* and reached the conclusion that the type "*Apatosaurus* specimen is merely a young animal of the form represented in the adult *Brontosaurus* specimen." . . . "As the term '*Apatosaurus*' has priority, '*Brontosaurus*' will be regarded as a synonym."

In regard to the species he says: "The species *A. ajax* cannot be recognized in the adult; *A. excelsus* is probably a synonym of *A. laticollis*; *A. amplus* is valid."

After reviewing the evidence in this whole matter in conjunction with this study of the very complete type skeleton of *Apatosaurus louisæ*, and of other specimens in the Carnegie Museum, I find no reasons for not accepting the determination of Riggs as being a correct and logical interpretation of the facts.

Although it is outside the scope of the present paper to attempt a revision of the genera or of the several described species, the acceptance of the above mentioned conclusion will explain my reference to specimens in the text as *Apatosaurus excelsus* (Marsh) instead of using the better and more widely known term of *Brontosaurus*.

The following species have been referred to *Apatosaurus*:

*Apatosaurus ajax* Marsh 1877

*A. grandis* Marsh 1877 = *Morosaurus grandis* 1879 =

*Camarasaurus grandis* 1921

*A. laticollis* Marsh 1879

*A. excelsus* (Marsh) 1879

*A. amplus* (Marsh) 1881

*A. louisæ* Holland 1915

*A. minimus* Mook 1917<sup>49</sup>

The number of these species that may be considered valid can only be determined by a careful study and comparison of the type specimens which will be

<sup>47</sup>Ibid., XVII, pp. 86-88, Pl. IV, fig. 1, 1879.

<sup>48</sup>Riggs, E. S., Field Columbian Museum, Pub. 82, Geol. ser., 1903, II, No. 4, p. 170.

<sup>49</sup>Mook, C. C., Bull. Amer. Mus. Nat. Hist., XXVII, 1917, Art. XVI, pp. 357-358, fig. 1.



done by Prof. H. F. Osborn and his associates who have a monographic study of the Sauropoda in preparation.

In this connection, however, attention should be called to a recent paper by Dr. F. von Huene,<sup>50</sup> in which he recognizes only three species in the genus *Apatosaurus*, i.e., *A. ajax*, *A. montanus* and *A. louisæ*. He regards the genera *Brontosaurus* and *Atlantosaurus* both to be synonyms of *Apatosaurus*. In this treatment of the genera he is obviously in error, for if the species *montanus* (originally *Atlantosaurus montanus*) is to be retained as a valid species, the genus *Atlantosaurus* must also be retained since it has priority over *Apatosaurus*. That the genus *Apatosaurus* should eventually prove to be a synonym of *Atlantosaurus* is not improbable. For the present, however, I propose to continue the use of *Apatosaurus* and shall regard the species *excelsus* as also being valid.

#### SUMMARY OF THE OSTEOLOGICAL FEATURES OF THE GENUS *APATOSAURUS*

*Skull and jaws* not certainly known.

*Vertebral column* composed of one hundred and fourteen vertebræ, divided as follows: Fifteen cervicals; ten dorsals; five sacrals; eighty-two caudals. Cervicals beginning with the sixth have divided spines; cervicals with heavy coalesced cervical ribs; cervicals reaching greatest length in the eleventh. Dorsal vertebræ heavy; spines posterior to the sixth, simple, high; anterior spines strongly divided; capitular facet retained on either third or fourth dorsal centrum; centra all opisthocœlus; sacrum with tall spines, from two to four fused into a plate; anterior caudals with tall simple spines; development of caudal ribs moderate disappearing posteriorly between eleventh and fifteenth vertebræ; anterior vertebræ short; all massive; true pleurocœls absent, distal caudals rod-like.

*Ribs* of thorax long and heavy; cervical ribs short, seldom equaling length of centrum, very robust, with or without projecting process in front of tuberculum.

*Pelvis*; pubis, heavy; pubic foramen closed, ischium with expanded distal end, often coalesced with ischium.

*Pectoral arch*; scapula with little expansion of distal end.

*Carpus* with one ossified carpal (scapho-lunar) found above metacarpals II, III, and IV.

*Manus* with five digits; clawed ungual on digit I; phalangial formula, 2, 2, 2, 1, 1.

*Femur* stout; fourth trochanter above middle.

*Tibia* stout with heavy recurved outer process; tibia and fibula less than length of femur.

*Tarsus* with one ossified tarsal, the astragalus; calcaneum absent.

*Pes* with five functional digits, first three bear unguals; first metatarsal stout, phalangial formula 2, 3, 4, 2, 1.

<sup>50</sup>Huene, F. v., Monog. zur. Geol. und Paleont., p. 288, 1932.

## DISCUSSION OF THE SPECIES

After a study of the two specimens of *Apatosaurus* considered in the preceding pages it is my conclusion that they represent two distinct species, *Apatosaurus louisæ* Holland and *A. excelsus* (Marsh) both of which can be adequately characterized. Whether they can be satisfactorily distinguished from the other described species of the genus, inadequately known at the present time, must await a restudy of the type materials, an investigation beyond the scope of the present paper.

In a preliminary paper<sup>51</sup> by Hatcher based on portions of specimen No. 563 C. M., no attempt was made to identify it as to species. It was referred by him to *Brontosaurus* here regarded as a synonym of *Apatosaurus*. After study and a comparison of this specimen, bone by bone, with a considerable number of unpublished plates illustrating skeletal parts of the type of *Brontosaurus excelsus*, that were available to me, such close agreement was found in their essential characteristics as to leave no doubt of their being conspecific. Furthermore, this specimen was found to be in almost full accord with the Field Museum specimen so well described and illustrated by Riggs,<sup>52</sup> which was identified by him as pertaining to the species *A. excelsus* after a study of the type skeleton in the Peabody Museum.

In establishing<sup>53</sup> the species, *A. louisæ*, Holland briefly listed those skeletal characters which in his estimation distinguished this species from *A. (Brontosaurus) excelsus* of Marsh.

In condensed form these were as follows:

1. Higher position of the pleurocœls on the side of the centra of the dorsal vertebræ.
2. A reduction in number of the anterior dorsal vertebræ having strongly developed hemispherical balls.
3. Non-fenestration of the transverse processes of the anterior caudals.
4. Higher position of the parapophysial facets of the dorsal vertebræ.
5. More perpendicular position of the spines of the mid-caudal vertebræ.

It is now possible to strengthen this preliminary characterization with additional skeletal features that taken together appear to adequately distinguish this species. These are graphically contrasted in the parallel columns below.

<sup>51</sup>Hatcher, J. B., *Annals Carnegie Museum*, I, 1902, pp. 356-376.

<sup>52</sup>Riggs, E. S., *Field Columbian Museum, Geol. Ser.*, Vol. II, No. 4, 1903, pp. 165-196.

<sup>53</sup>Holland, W. J., *Annals Carnegie Museum*, vol. X, 1915, pp. 144-145.



## APATOSAURUS LOUISÆ

1. Cervical Vertebrae.
  - (a). Cervical ribs without forwardly projecting process.
  - (b). Infrapostzygapophysial cavity posterior to C5, undivided by accessory lamina.
2. Dorsal Vertebrae.
  - (a). Relatively slender transverse processes on anterior half of dorsal series.
  - (b). Capitular facet reaches extreme height on D5.
  - (c). Hyposphen-hypantrum articulation first appears on D3.
  - (d). Hyposphen reaches its maximum development on D4.
  - (e). Transverse and vertical diameters of posterior end of centra subequal.
  - (f). Centrum of D2 longest of series.
3. Caudal Vertebrae.
  - (a). Transverse processes of anterior caudals not perforated by fenestra.
  - (b). Spines of mid caudal region more erect.
  - (c). Vertical diameter of anterior caudal centra greater than transverse diameter.
  - (d). Caudal spines slender.
4. Sacrals.

Sacral ribs articulating only with half the length of the sacral centra.
5. Scapula.
  - (a). Spine diagonal to axis of greatest length.
  - (b). Muscular fossa above spine much reduced.
  - (c). Distal portion of blade but little expanded.

## APATOSAURUS EXCELSUS

1. Cervical vertebrae.
  - (a). Cervical ribs with a forwardly projecting process.
  - (b). Infrapostzygapophysial cavity posterior to C5, subdivided by accessory lamina.
2. Dorsal Vertebrae.
  - (a). Relatively heavy transverse processes on anterior half of dorsal series.
  - (b). Capitular facet reaches extreme height on D6.
  - (c). Hyposphen-hypantrum articulation first appears on D4.
  - (d). Hyposphen reaches its maximum development on D6.
  - (e). Transverse diameter of centra exceeds vertical diameter.
  - (f). Centrum of D1 longest of series.
3. Caudal Vertebrae.
  - (a). Transverse process of anterior caudals perforated by fenestra.
  - (b). Spines of mid caudal region less erect.
  - (c). Diameters of anterior caudals subequal.
  - (d). Caudal spines stout.
4. Sacrals.

Sacral ribs articulating with full length of sacral centra.
5. Scapula.
  - (a). Spine at right angles to axis of greatest length.
  - (b). Muscular fossa above spine large.
  - (c). Distal portion of blade somewhat expanded both anteriorly and posteriorly.

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## EXPLANATION OF PLATE XXI.

- FIG. 1. Dinosaur National Monument Quarry. The series of caudal vertebræ of *Apatosaurus louisæ* (No. 3018 C. M.) in the middle foreground was the initial discovery that led to the development of this great quarry. In uncovering this skeleton of *Apatosaurus* other specimens were encountered and so it continued during the entire thirteen years that collecting was carried on here by the Carnegie Museum.
- FIG. 2. A complete backbone of *Apatosaurus* (Quarry No. 160, Cat. No. 3378 C. M.) in the process of exhumation by Carnegie Museum collectors. The four-foot squares outlined on the rock face are for the purpose of accurately plotting the fossils on the quarry map.
- FIG. 3. Showing the method of removing large blocks of plaster-encased bones from the quarry to a point accessible to wagons.
- FIG. 4. Removing the overburden from the face of the fossil-bearing sandstone on the east side of the quarry. The late Dr. W. J. Holland standing at the entrance to the excavation.
- FIG. 5. Showing the method used in lowering large bones from the steeply inclined face of the quarry by use of block and fall.
- FIG. 6. Face of quarry showing a specimen of *Diplodocus* (Quarry No. 150) partly uncovered. The large size of the bones is indicated by comparison with the man seated in the right foreground.
- FIG. 7. General view, looking eastward from the Dinosaur National Monument Quarry toward Split Mountain.
- FIG. 8. Showing one of the methods used in handling the heavy blocks of stone enclosed fossils.
- All photographs by Earl Douglass.











## EXPLANATION OF PLATE XXII.

- FIG. 1. Dinosaur National Monument Quarry looking toward the east. The fossil-bearing layer has been largely removed from the sloping wall on the left of the picture. The track was used for a mine car on which debris was removed to the dump.
- FIG. 2. Looking upward to the east end of the Dinosaur Quarry, showing trail down which boxes of specimens were dragged. The dump may be seen in the upper middle of the picture, and boxes of specimens ready for shipment in the lower foreground.
- FIG. 3. East side of Dinosaur Quarry, as it appeared at the time of suspension of work by the Carnegie Museum collectors. The skeleton (*Diplodocus*) in the rock at the right of the photograph was turned over to the Smithsonian Institution in 1923. The vertebræ (*Barosaurus*) under the canopy were collected by the University of Utah and are now in the American Museum of Natural History, New York City. All photographs by Earl Douglass.











## EXPLANATION OF PLATE XXIII.

Quarry map of the Dinosaur National Monument, showing the position of the skeleton of *Apatosaurus louisæ*, and the relative positions of all important specimens collected there.

On the map the horizontal lines are lettered and the perpendicular lines are numbered. The numbers indicate the number of feet distant from a zero line near the middle of the quarry. For example, 4, 8, and 12, etc., indicate distances west of zero, and E 4, E 8, E 12, etc., indicate distances east of the zero line. To locate a specimen on the map such as the type of *Apatosaurus louisæ*, it will be found to lie in the intersection of perpendicular lines 4 to 56 and the horizontal lines D to H.

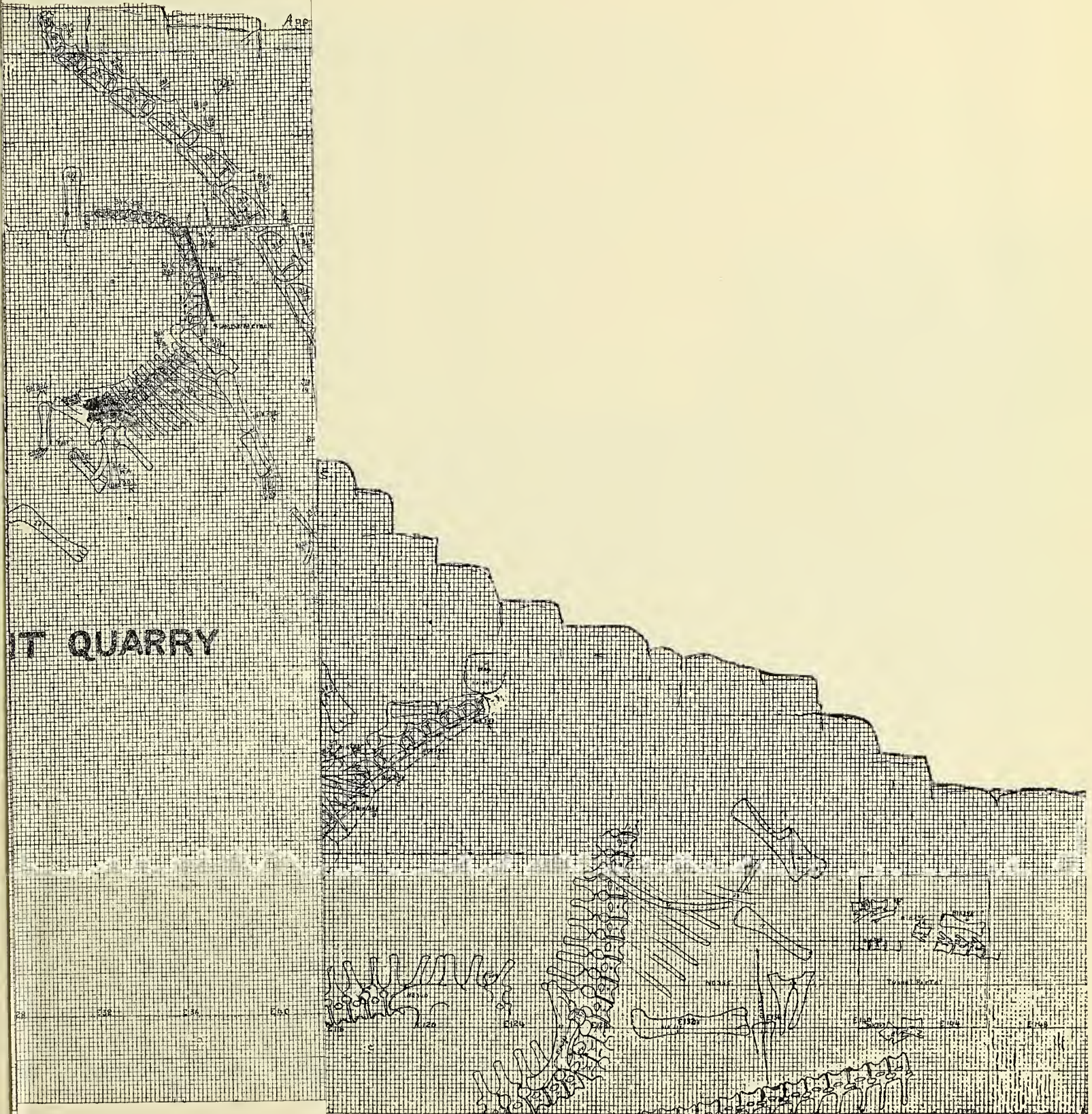
Specimens were numbered consecutively as found, beginning with No. 1, which is the *A. louisæ* skeleton. Likewise the scattered bones of an individual were also numbered. Thus a bone of specimen No. 25 might be assigned the number 10, if so, it would be designated  $\frac{25}{10}$ ; occasionally letters were used, then this same bone would be designated  $\frac{25}{B}$ . So far as it was feasible to do so, in the field, a single number was applied to all parts of an individual. Below is a list of the more important identified specimens, accompanied by the letters and figures which locate them on the map.

## LIST OF THE MORE IMPORTANT SPECIMENS AS SHOWN ON THE QUARRY MAP.

Quarry No.		Cat No.	Location on Map
1	<i>Apatosaurus louisæ</i> Holland Type.....	3018 C. M.	D to H. & 4-56
24	Herbivorous dinosaur (small) .....		G-46
26	<i>Dryosaurus altus</i> Marsh .....	3392 C. M.	A-15e
39	<i>Stegosaurus</i> sp.....		A to F-10-20e
40	<i>Apatosaurus</i> ?.....		B to E-2-W 48
58	<i>Glyptops utahensis</i> Gilmore Type.....	3412 C. M.	E-36
60	<i>Diplodocus</i> sp. sk. and mandible.....	11161* C. M.	C to D-36
89	Sauropod.....		BC-8
90	<i>Diplodocus</i> sp.....		E-9
95	<i>Glyptops</i> .....	3411 C. M.	C-52
130	Sauropod.....		B-56
145	Sauropod.....		E-88
150	<i>Diplodocus</i> sp.....		C-100
150B	<i>Barosaurus</i> (Skeleton).....		C-100
154	<i>Glyptops utahensis</i> Gilmore Paratype.....	3380 C. M.	E-136
155	<i>Diplodocus</i> sp.....		E-108
160	<i>Diplodocus</i> -like skull.....	11162 C. M.	C to G-116-156
160	<i>Apatosaurus</i> sp. complete vertebral series.....	3378 C. M.	F-140
202	<i>Antrodemus</i> sp.....		B to C-96
210	Sauropod.....		Z to B-76-102
214	Sauropod (small).....		B-122
220	<i>Diplodocus</i> sp. (skull, neck).....	3452 C. M.	Y to B-112-117
230	Crocodile (skull).....		Y-130
240	<i>Camarasaurus</i> sp.....	11393 C. M.	Y-132
272	Turtle.....		V-144
301	<i>Camarasaurus</i> sp.....		A to D-36-E
310	<i>Brachyosaurus</i> ?.....		D to F-40e
324	<i>Camarasaurus</i> sp.....		E-65e
325	<i>Uintasaurus douglassi</i> Holland Type.....	11068 C. M.	A-46e
333	<i>Camarasaurus lentus</i> (Marsh) (skeleton).....		A-72e
340	<i>Barosaurus</i> sp. skeleton in Amer. Mus. Nat.Hist.....		U to X-116e
350	<i>Stegosaurus</i> sp.....		X-108e
355	<i>Diplodocus longus</i> Marsh in U. S. Nat. Mus.....	10865 U. S. N. M.	V-128c
360	<i>Laosaurus gracilis</i> Marsh.....	11340 C. M.	U-101e
351	<i>Diplodocus</i> sp. skull small.....	11255 C. M.	U-156e
370	<i>Camptosaurus medius</i> Marsh (skeleton).....	11337 C. M.	V-94e

\*Gilmore, C. W. Memoirs Carnegie Museum, vol. X, No. 3, 1925, erroneously refers to this skull as No. 11255 C. M.

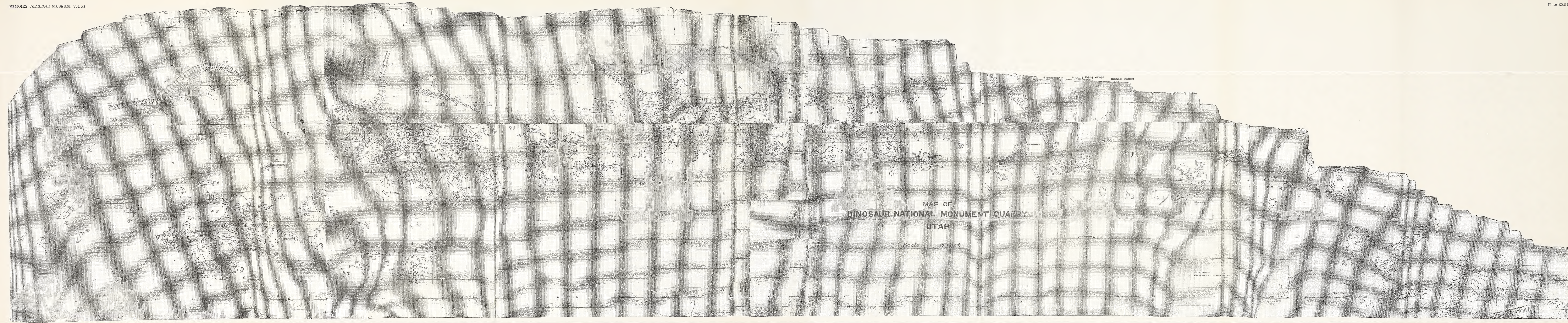




















## EXPLANATION OF PLATE XXIV.

Cervical vertebræ of *Apatosaurus louisæ*. Type, No. 3018 C. M., Cervicals 1 to 15 inclusive. *A.* anterior views; *B.* lateral views; *C.* posterior views; cervicals 6, 7, 8, 9, and 10, have had some of their lateral structure drawn from the right side. Cervicals 13, 14, and 15, have been much restored from badly crushed originals, and should be used with caution.

*A. C.*, anterior convexity.

*A. L.*, accessory lamina.

*At.*, Atlas.

*Ax.*, Axis.

*Cv. R.*, Cervical rib.

*Di.*, Diapophysis.

*H. L.*, Horizontal lamina.

*Id. C.*, Infradiapophysial cavity.

*Ipod. L.*, Infrapostdiapophysial lamina.

*Ipoz. C.*, Infrapostzygapophysial cavity.

*Ipoz. L.*, Infrapostzygapophysial lamina.

*Iprd. L.*, Infraprediapophysial lamina.

*Iprz. C.*, Infraprezygapophysial cavity.

*Iprz. L.*, Infraprezygapophysial lamina.

*Itrpoz. L.*, Intrapostzygapophysial lamina.

*Itrprz. L.*, Intraprezygapophysial lamina.

*Pa.*, Parapophysis.

*Pl.*, Pleurocœl.

*Psp. C.*, Postspinal cavity.

*Poz.*, Postzygapophysis.

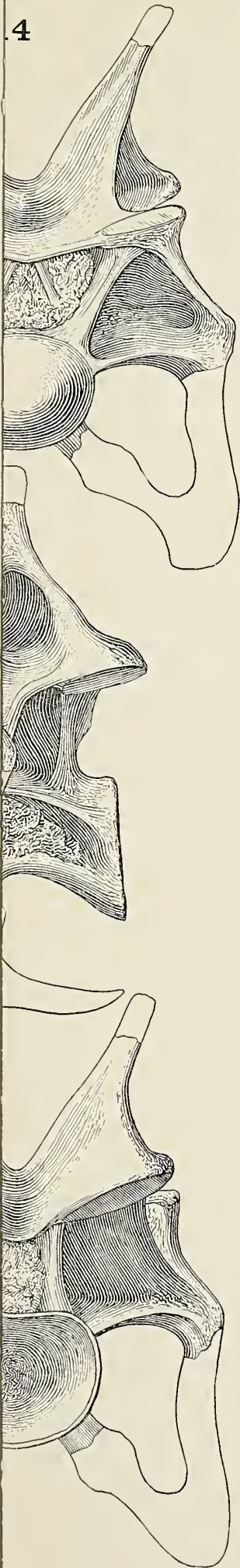
*Prz.*, Prezygapophysis.

*Spoz. L.*, Suprapostzygapophysial lamina.

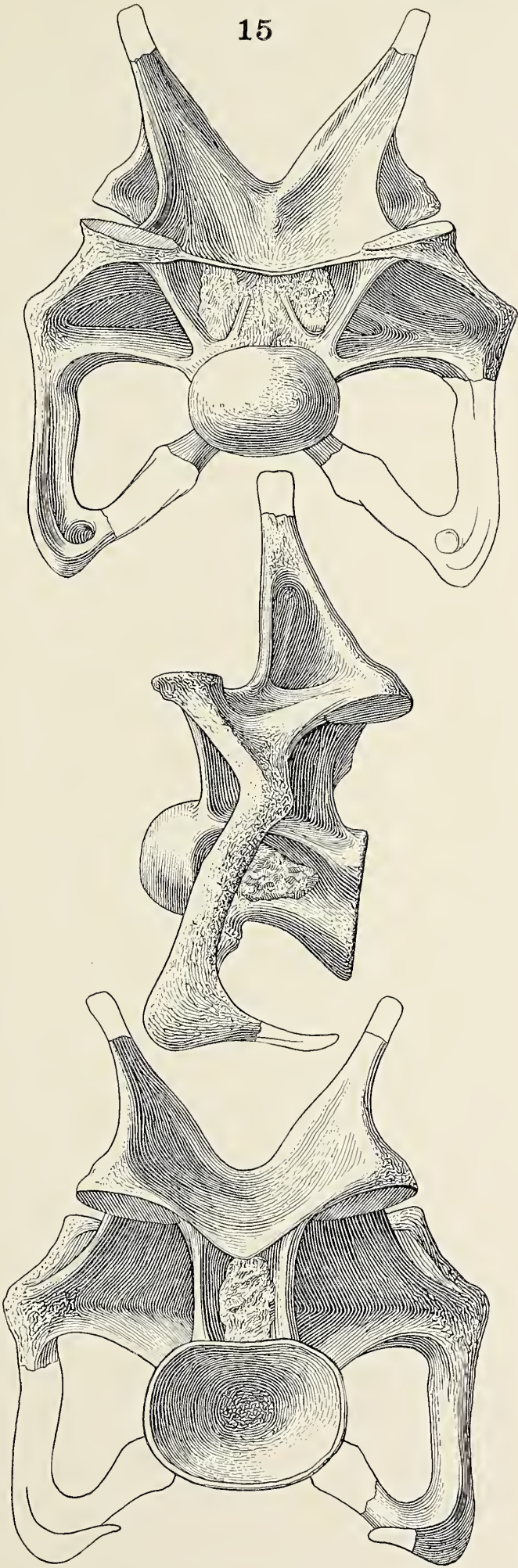
*Sprz. L.*, Supraprezygapophysial lamina.

All one-tenth natural size.

4



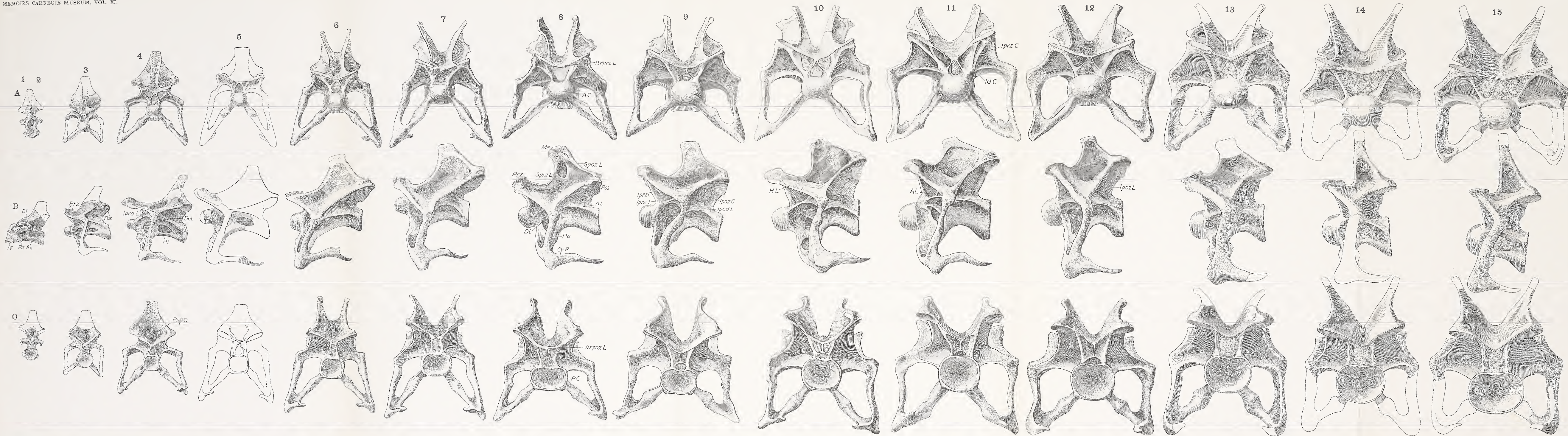
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## EXPLANATION OF PLATE XXV.

Dorsal vertebræ of *Apatosaurus louisæ*, Type, No. 3018 C. M. Dorsals 1 to 9 inclusive. A. anterior views; B. lateral views; C. posterior views. The figures indicate dorsals 1 to 9 respectively.

A. L., accessory lamina.

Di., diapophysis.

H. L., horizontal lamina.

Hypn., hypantrum.

Hyps., hyposphen.

Id. C., infradiapophysial cavity.

Id. L., infradiapophysial lamina.

Ipod. L., infrapostdiapophysial lamina.

Ipoz. C., infrapostzygapophysial cavity.

Iprd. L., infraprediapophysial lamina.

Iprz. C., infraprezygapophysial cavity.

Iprz. L., infraprezygapophysial lamina.

Me., metapophysis.

N. C., neural canal.

P. C., posterior concavity or cup.

Pa., parapophysis.

Pl., pleurocel.

Poz., postzygapophysis.

Prz., prezygapophysis.

Ps. L., prespinal lamina.

Sd. L., supradiapophysial lamina.

Sp., spine.

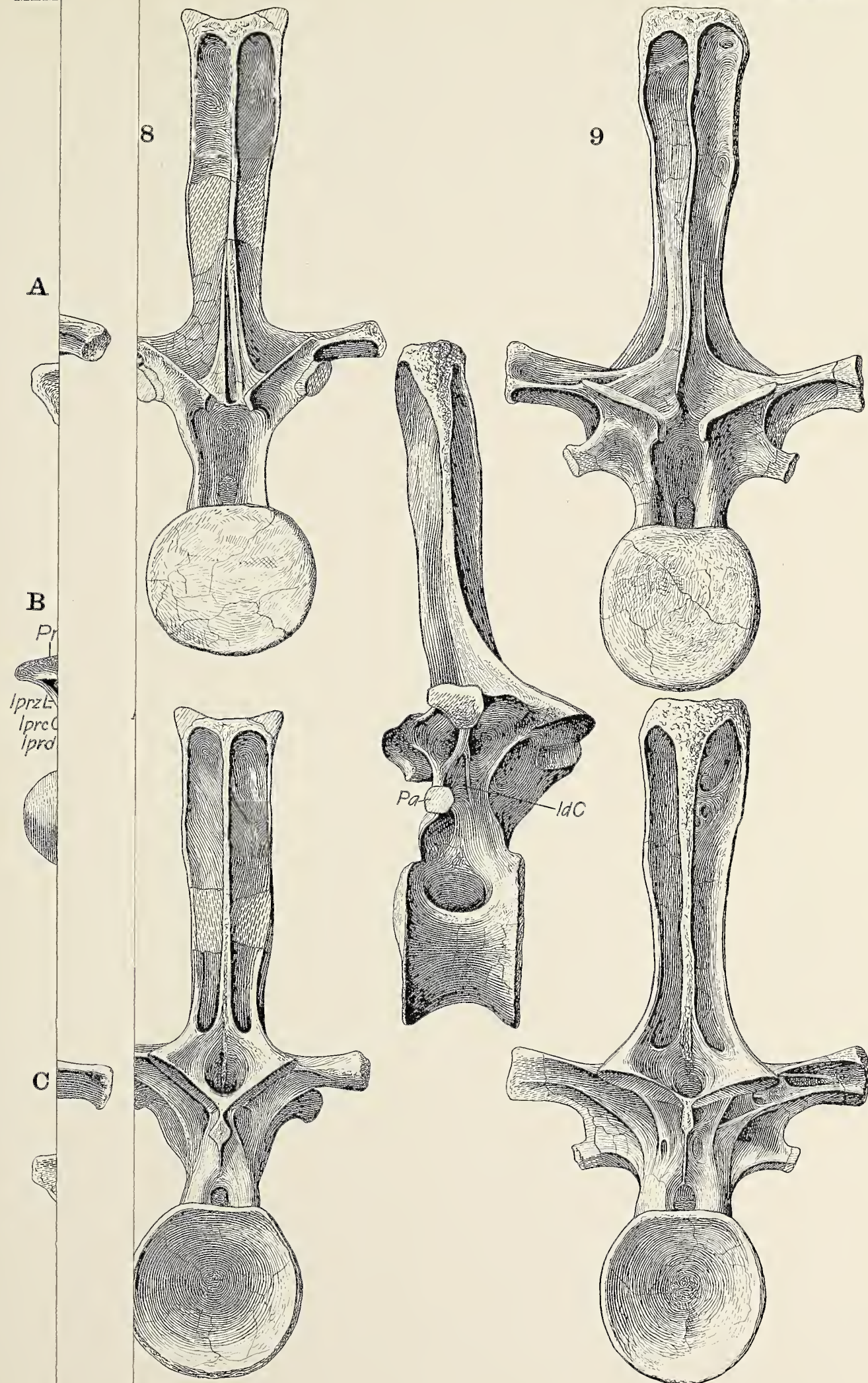
Spoz. C., suprapostzygapophysial cavity.

Spoz. L., suprapostzygapophysial lamina.

Sprz. C., supraprezygapophysial cavity.

Sprz. L., supraprezygapophysial lamina.

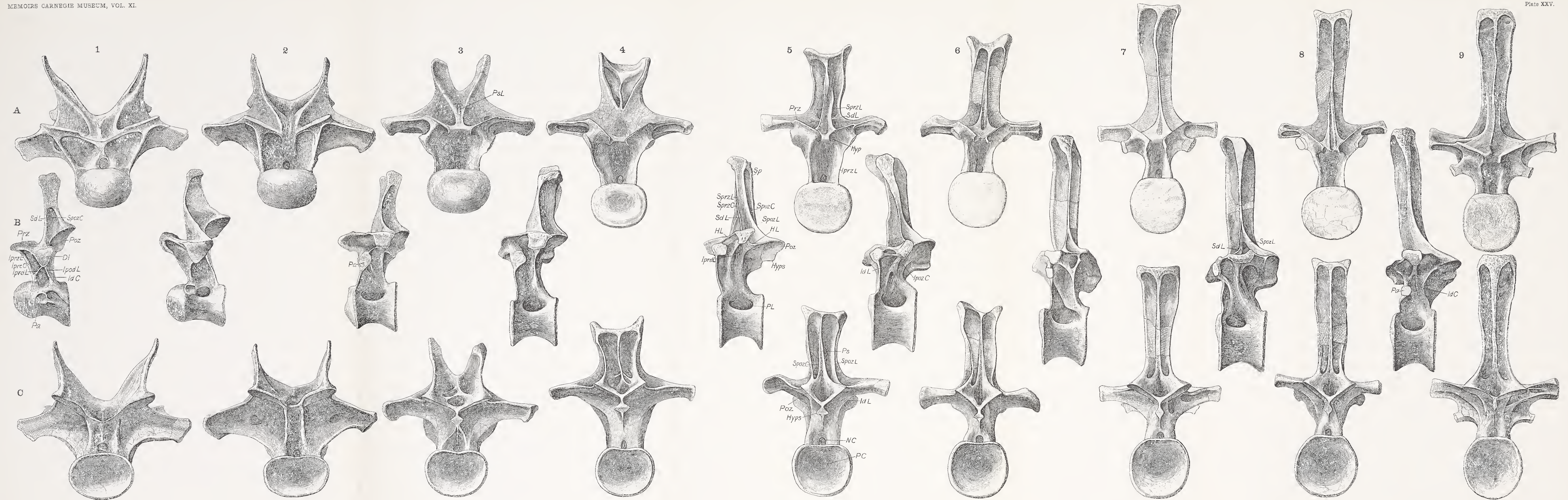
All one-tenth natural size.



















## EXPLANATION OF PLATE XXVI.

Caudal vertebræ of *Apatosaurus louisæ*. Type, No. 3018 C. M. Caudals one to fourteen inclusive.  
A. anterior view; B. lateral view; C. posterior views.

A. C., anterior concavity or cup.

Cd. R., Caudal rib.

Hyp., Vestigial hyposphen.

Iprz. L., infraprezygapophysial lamina.

N. C., Neural Canal.

Pos. L., Postspinal lamina.

Poz., Postzygapophysis.

Prs. L., Prespinal lamina.

Prz., Prezygapophysis.

Sp., Spine.

Spoz., Suprapostzygapophysial lamina.

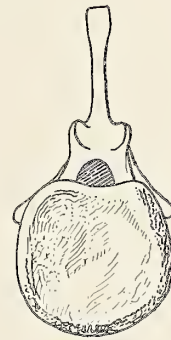
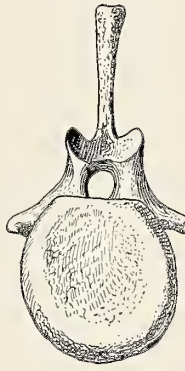
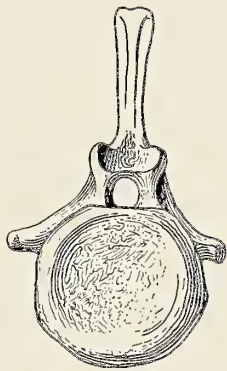
Sprz. L., Supraprezygapophysial lamina.

All one-tenth natural size.

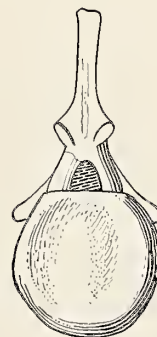
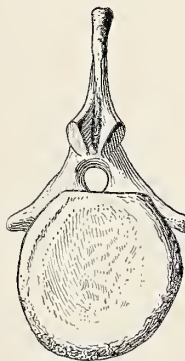
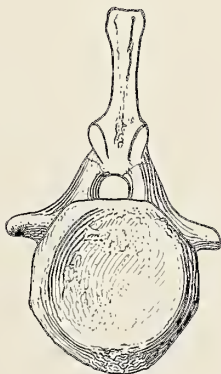
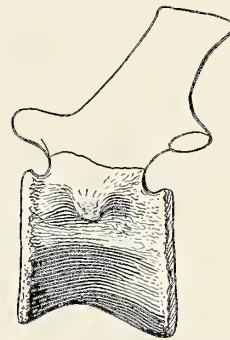
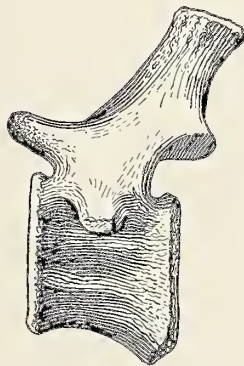
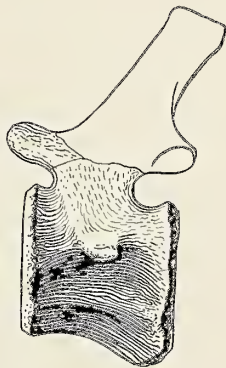
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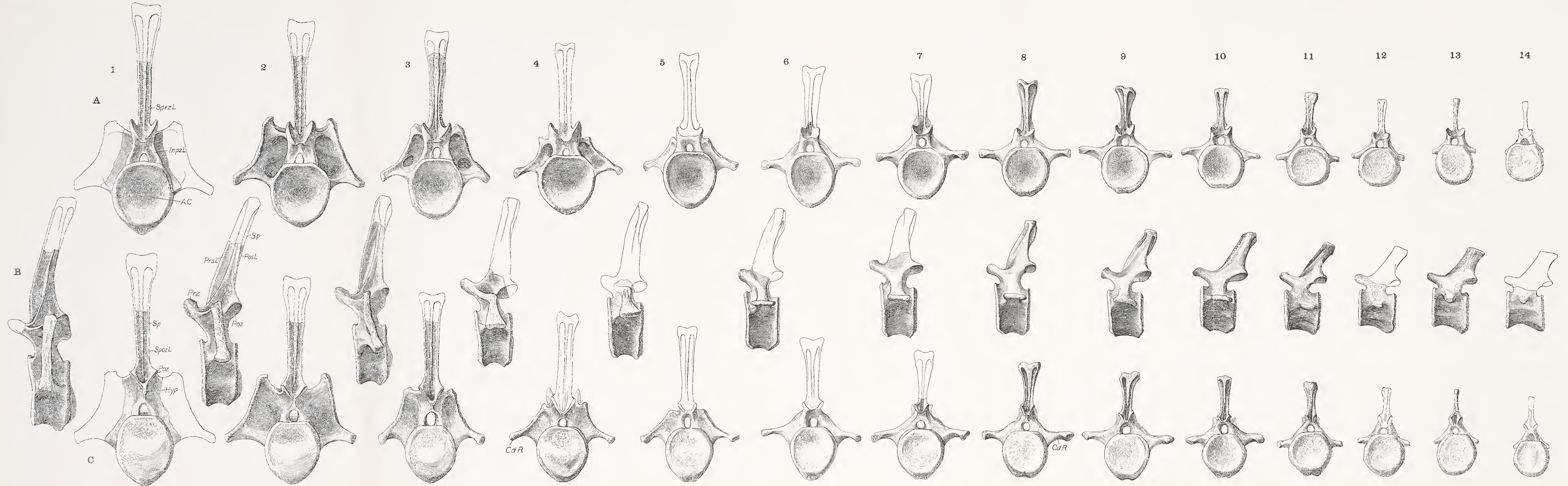


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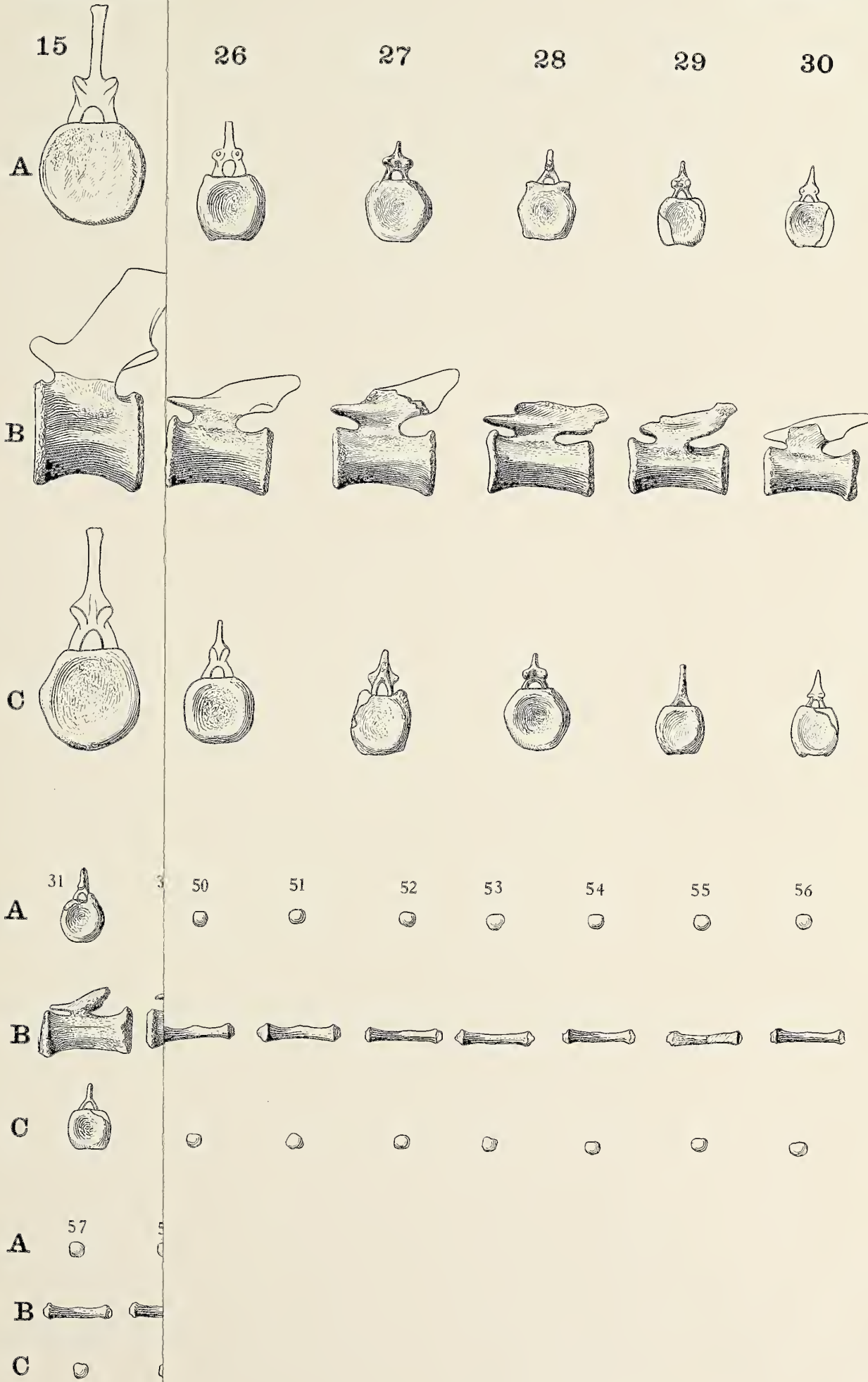




## EXPLANATION OF PLATE XXVII.

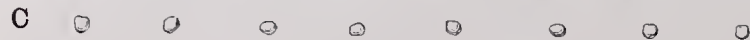
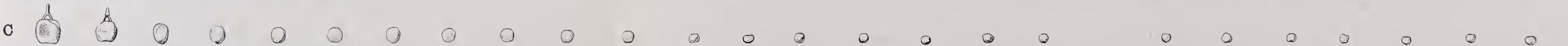
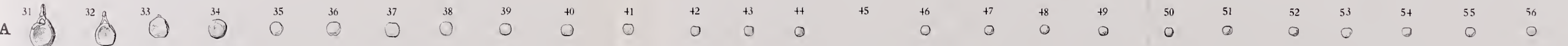
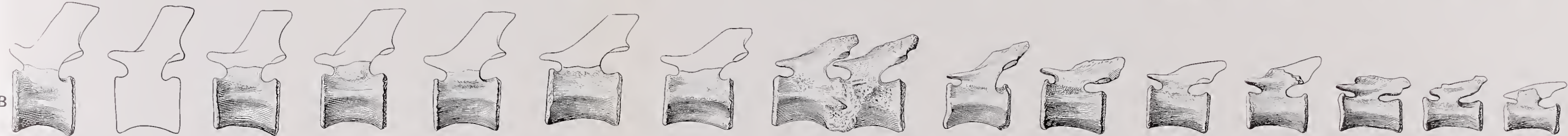
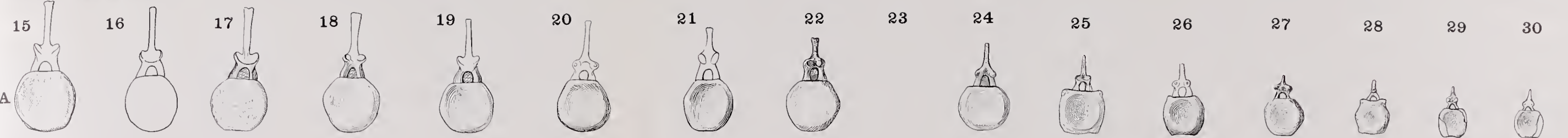
Caudal vertebræ of *Apatosaurus louisæ*. Type, No. 3018 C. M. *A.* anterior views; *B.* lateral views; *C.* posterior views. The figures 15-64 indicate caudals fifteen to sixty-four respectively.

All one-tenth natural size.













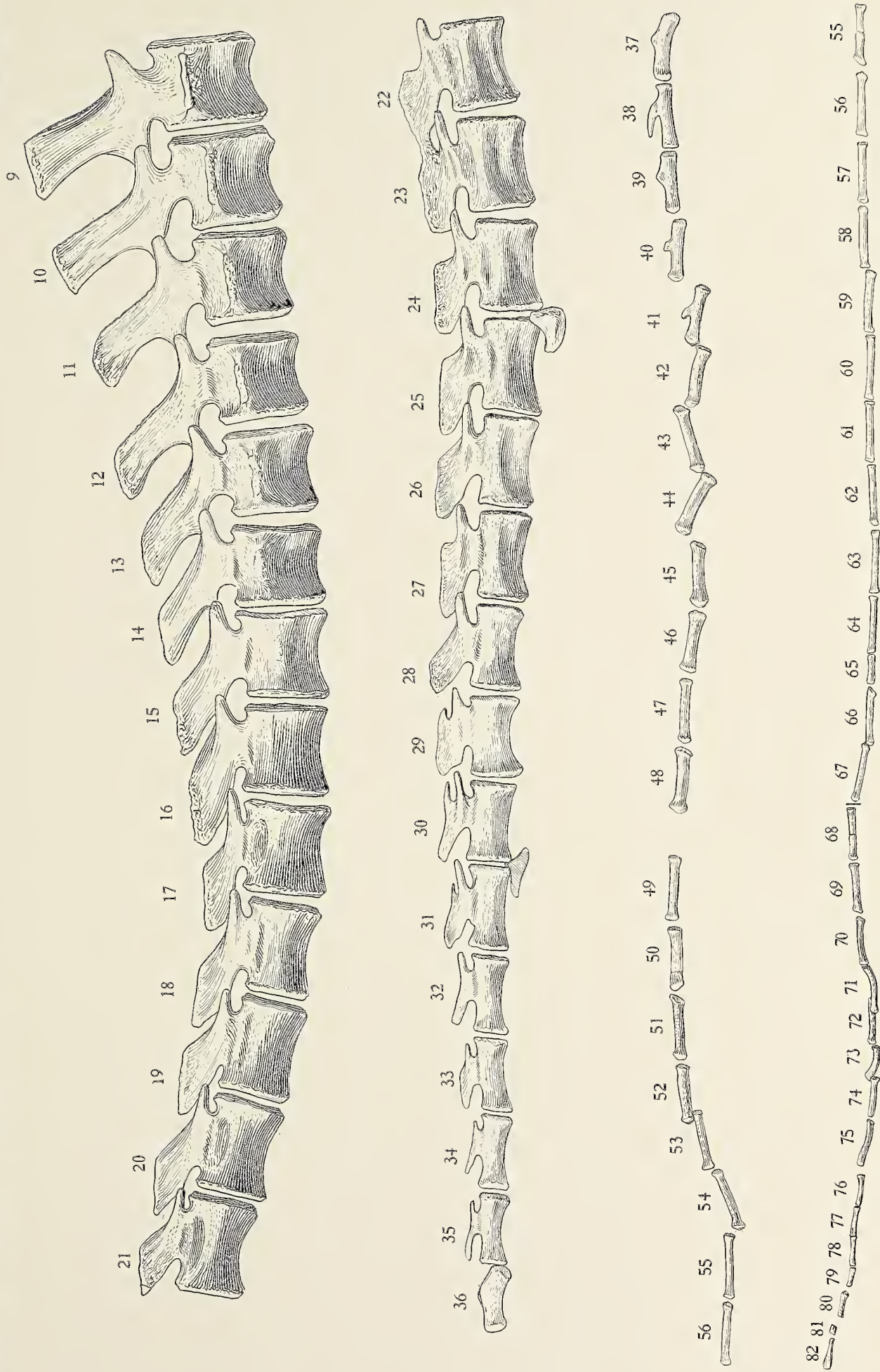




## EXPLANATION OF PLATE XXVIII.

Caudal vertebræ of *Apatosaurus* sp., No. 3078 C. M. Caudals 9 to 82 inclusive. A portion of the complete articulated vertebral series, shown *in situ*, fig. 2., Plate I.

All one-tenth natural size.







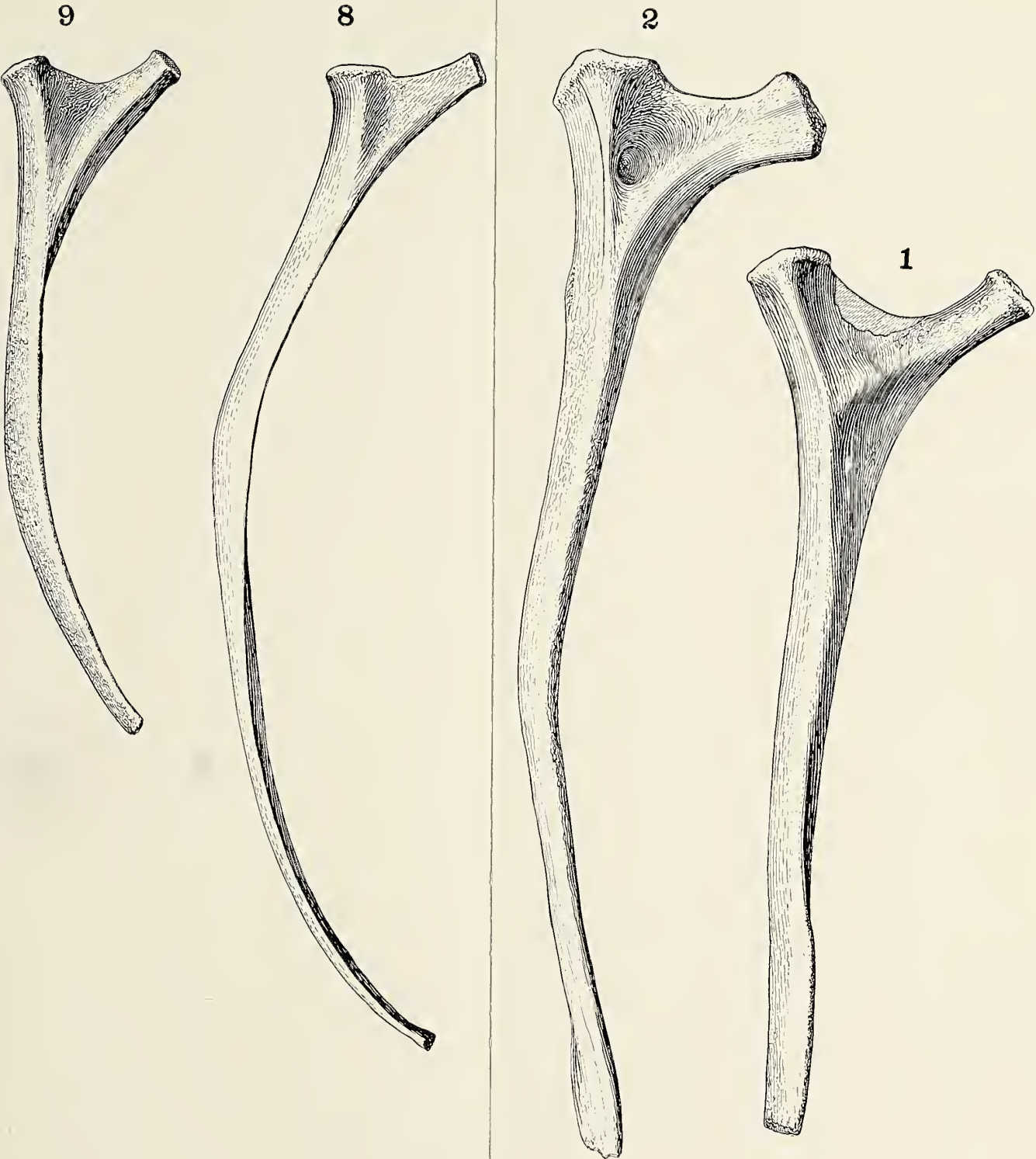




## EXPLANATION OF PLATE XXIX.

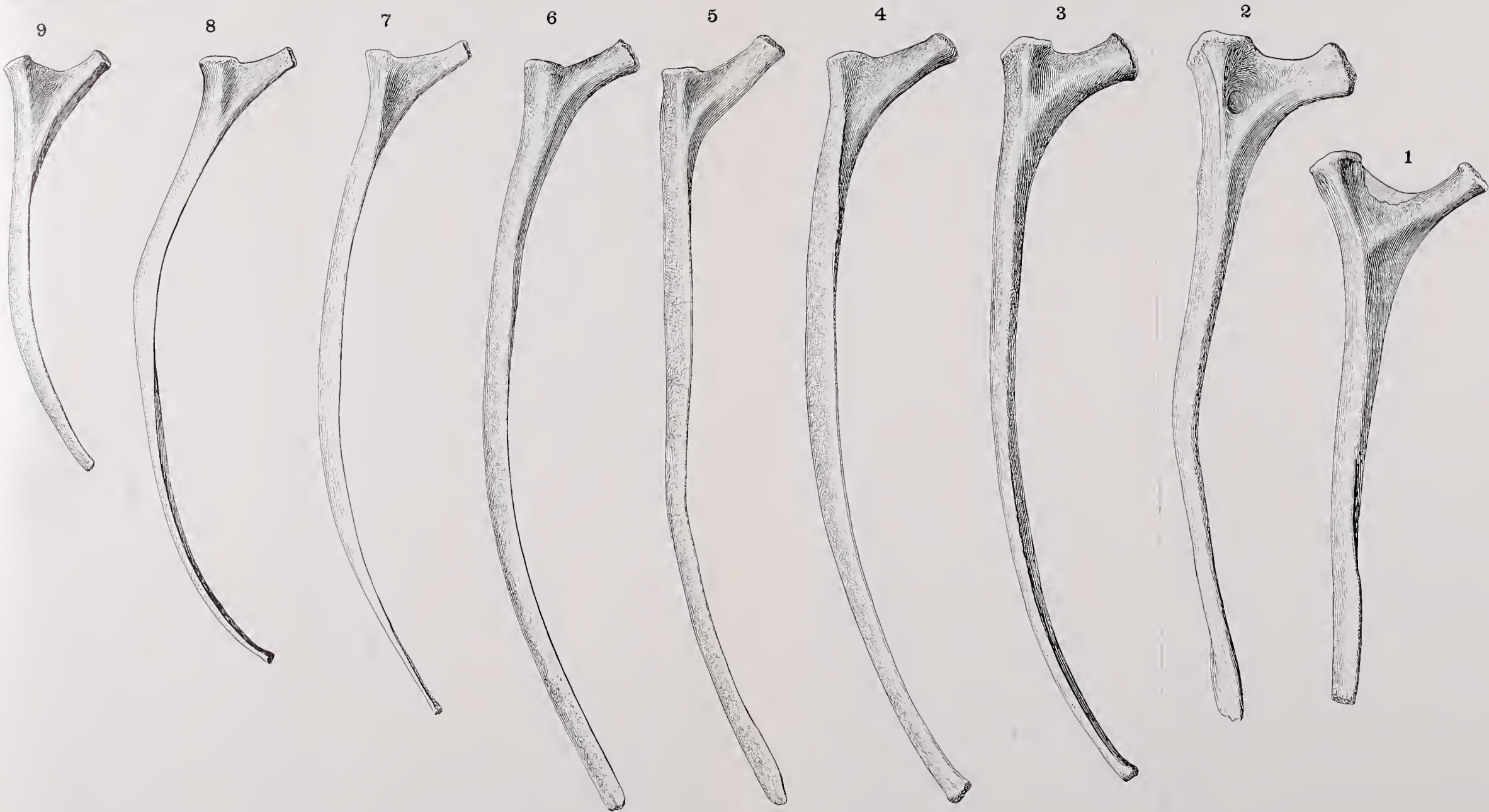
Dorsal ribs of right side of *Apatosaurus louisæ*. Type, No. 3018 C. M. Ribs one to nine respectively. Viewed from the front.

All one-tenth natural size.

















## EXPLANATION OF PLATE XXX.

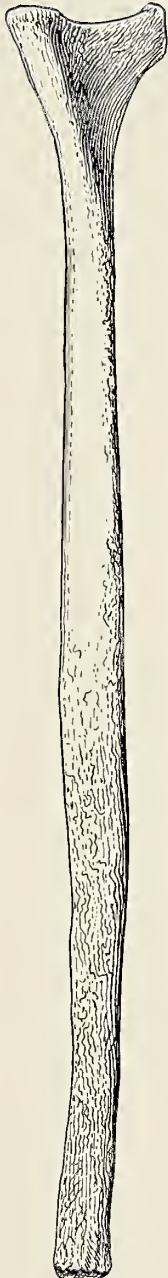
Dorsal ribs of right side of *Apatosaurus louisæ*. Type, No. 3018 C. M. Ribs one to nine respectively.  
Lateral view.

All one-tenth natural size.

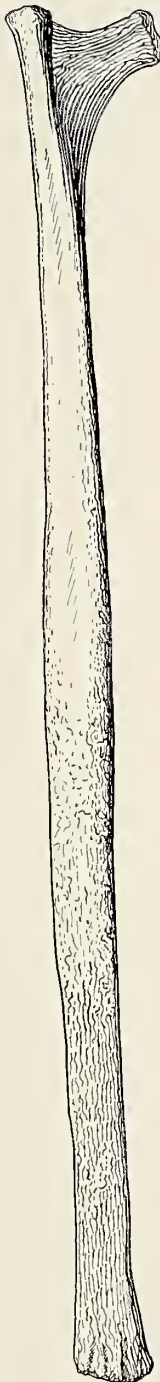
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7

















## EXPLANATION OF PLATE XXXI.

Cervical vertebræ of *Apatosaurus excelsus*. No. 563 C. M. A. anterior views; B. lateral views; C. posterior views. Cervicals 3, 4, 5, 7, 8, 9, 13?, and 15 respectively. These have been provisionally determined by comparison with the articulated series of *A. louisæ*.

A. C., anterior convexity.

A. L., accessory lamina.

Cv. R., cervical rib.

Di., diapophysis.

H. L., horizontal lamina.

Ipod. L., infrapostdiapophysial lamina.

Ipoz. C., infrapostzygapophysial cavity.

Ipoz. L., infrapostzygapophysial lamina.

Iprd. L., infraprediapophysial lamina.

Iprz. C., infraprezygapophysial cavity.

Iprz. L., infraprezygapophysial lamina.

Intrpoz. L., infrapostzygapophysial lamina.

Itrprz. L., intraprezygapophysial lamina.

Me., metapophysis.

Pa., parapophysis.

Pl., pleurocœl.

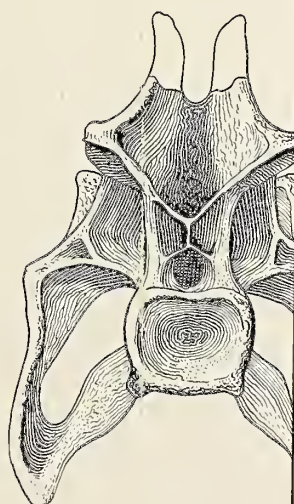
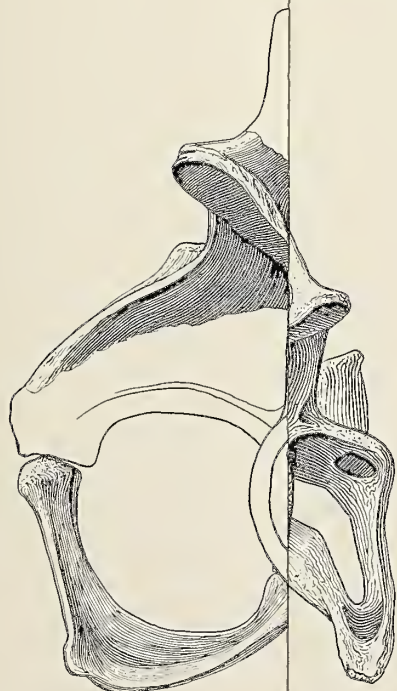
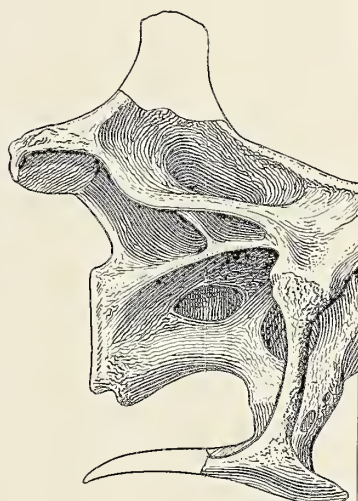
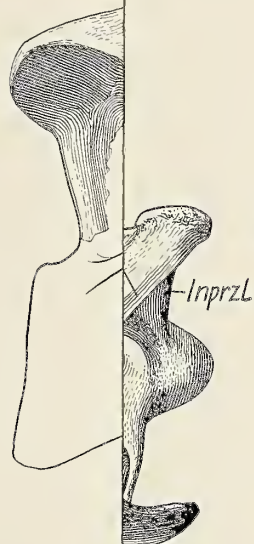
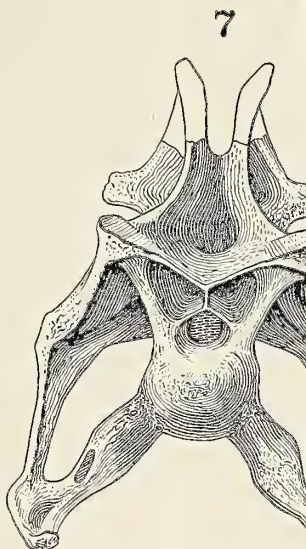
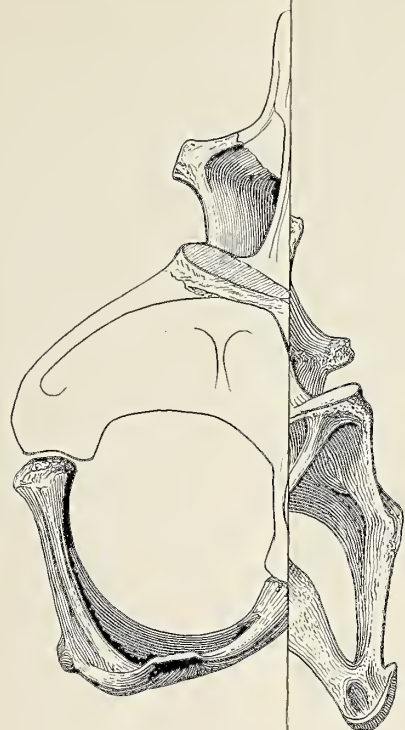
Poz., postzygapophysis.

Prz., prezygapophysis.

Spoz. L., suprapostzygapophysial lamina.

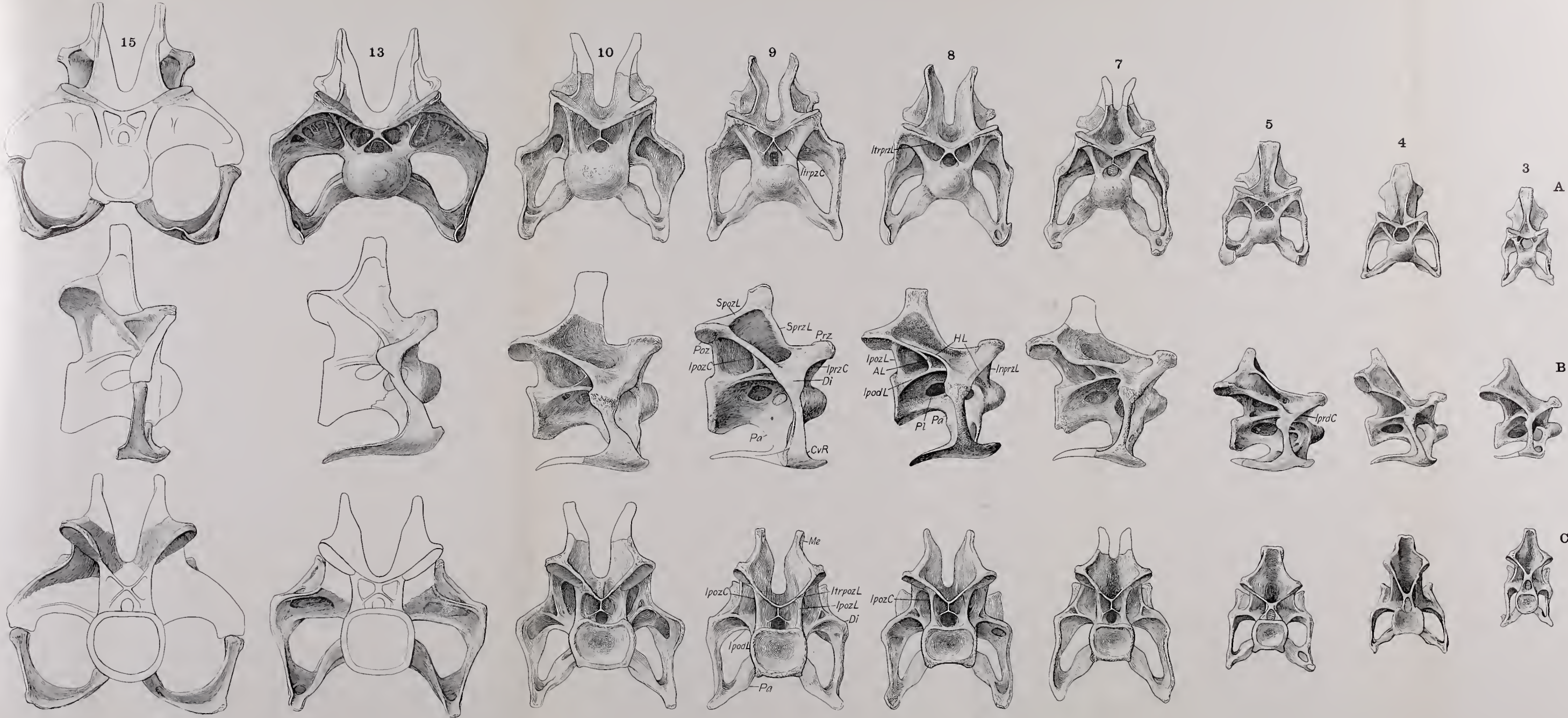
Sprz. L., supraprezygapophysial lamina.

All one-tenth natural size.















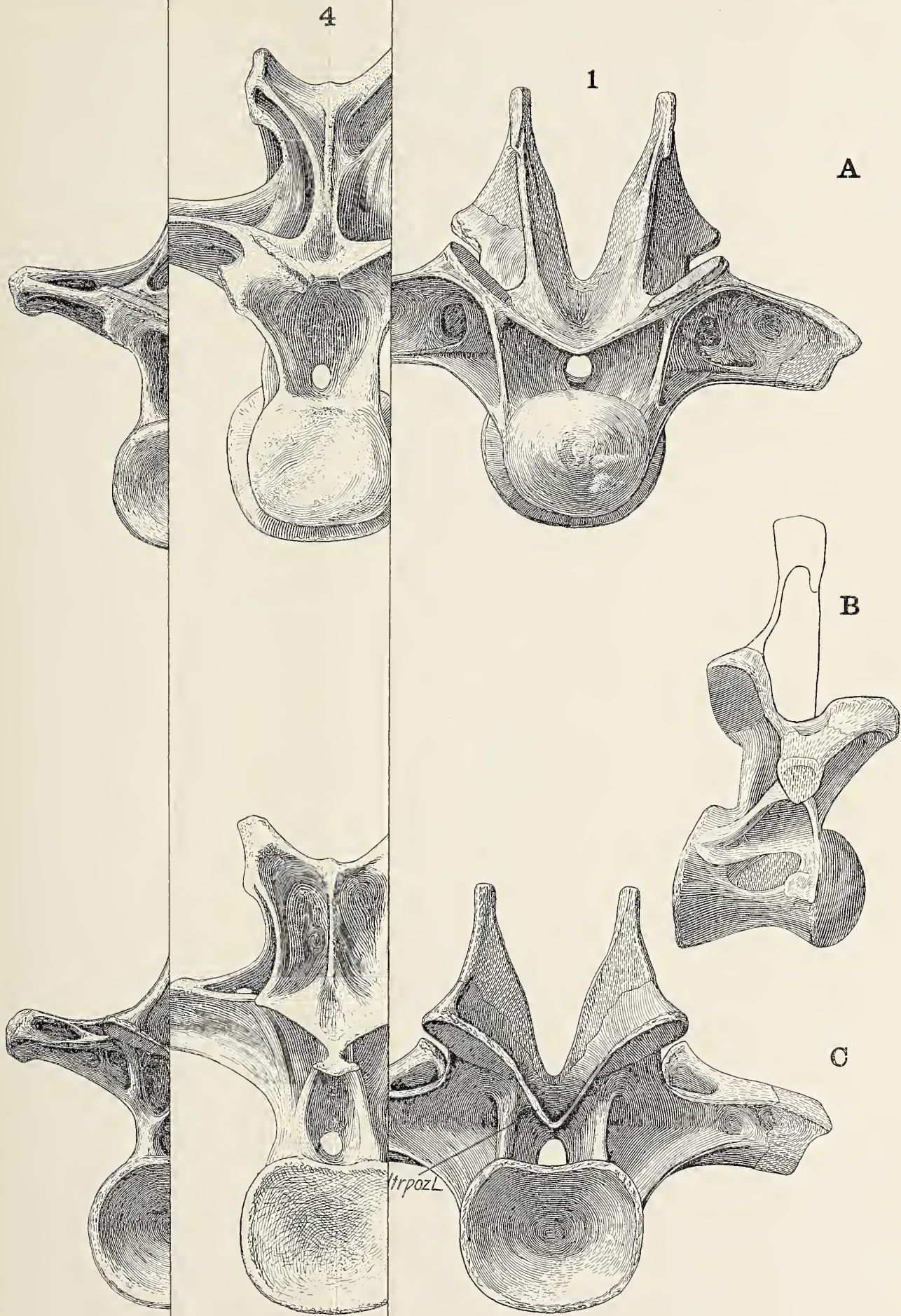


## EXPLANATION OF PLATE XXXII.

Dorsal vertebrae of *Apatosaurus excelsus*. No. 563 C. M. Dorsals 1 to 9 inclusive. *A.* anterior views; *B.* lateral views; *C.* posterior views. The original association is unknown, so that their arrangement here, especially the posterior members may be regarded as provisional. 1, 2, 3, 4, 5, 6, 7, 8, and 9, dorsal vertebrae one to nine respectively.

- A. L.*, accessory lamina.
- Di.*, diapophysis.
- H. L.*, horizontal lamina.
- Hyps.*, hyposphen.
- Id. C.*, infradiapophysial cavity.
- Ipod. L.*, infrapostdiapophysial lamina.
- Ipoz. C.*, infrapostzygapophysial cavity.
- Ipoz. L.*, infrapostzygapophysial lamina.
- Iprd. L.*, Infraprediapophysial lamina.
- Iprz. C.*, infraprezygapophysial cavity.
- Iprz. L.*, infraprezygapophysial lamina.
- Itrpoz. L.*, intrapostzygapophysial lamina.
- Itrprz. L.*, intraprezygapophysial lamina.
- Pa.*, parapophysis.
- Pl.*, pleurocel.
- Pod. L.*, postdiapophysial lamina.
- Poz.*, postzygapophysis.
- Prz.*, prezygapophysis.
- Sd. L.*, supradiapophysial lamina.
- Sp.*, spine.
- Spoz. L.*, suprapostzygapophysial lamina.
- Spoz. Cl.*, suprapostzygapophysial cavity.
- Sprz. L.*, supraprezygapophysial lamina.

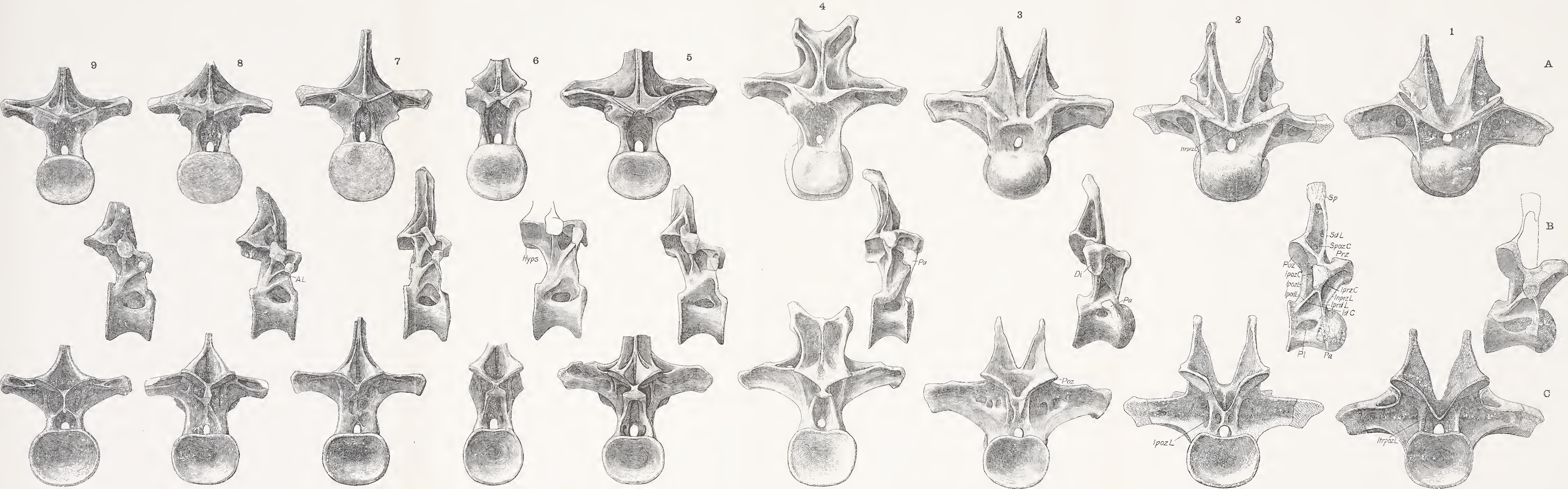
All one-tenth natural size.



















## EXPLANATION OF PLATE XXXIII

Caudal vertebræ of *Apatosaurus excelsus*, No. 563 C. M. These vertebræ were found disarticulated and scattered and are tentatively allocated in the caudal series. *A.* anterior view; *B.* lateral view; *C.* posterior view. Numerals 1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 13, 16, 17, 23, 25, 26, 30 and 31, caudal vertebræ one to nine, eleven, thirteen, sixteen, seventeen, twenty-three, twenty-five, twenty-six, thirty and thirty-one respectively.

All one-tenth natural size.

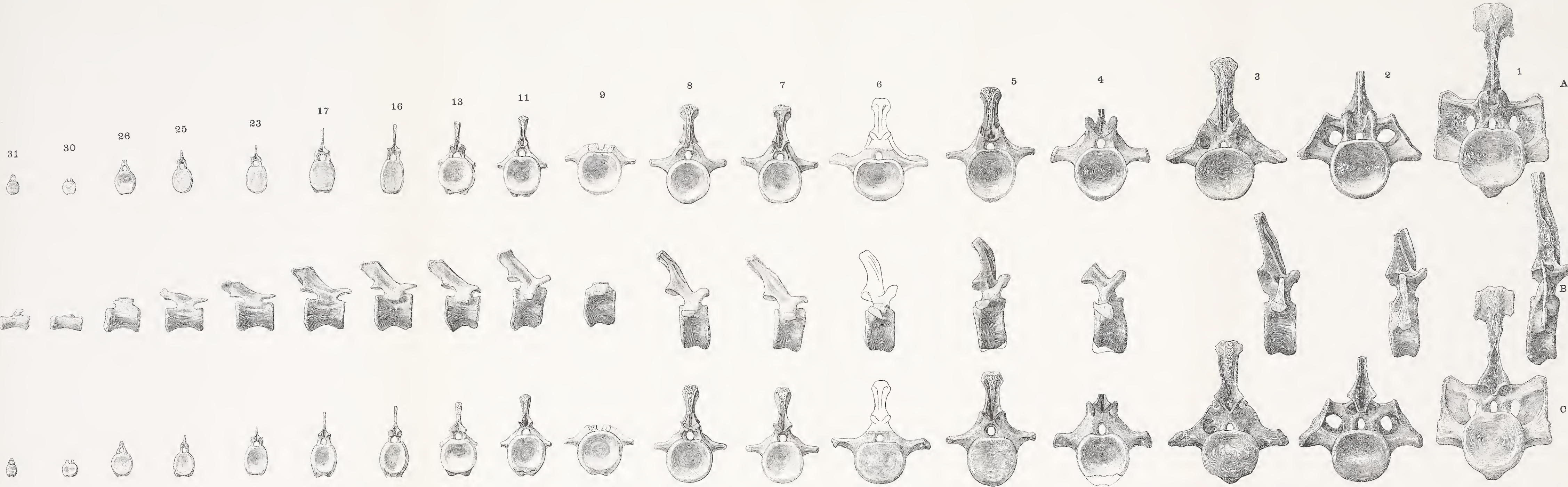
ME

3

















## EXPLANATION OF PLATE XXXIV.

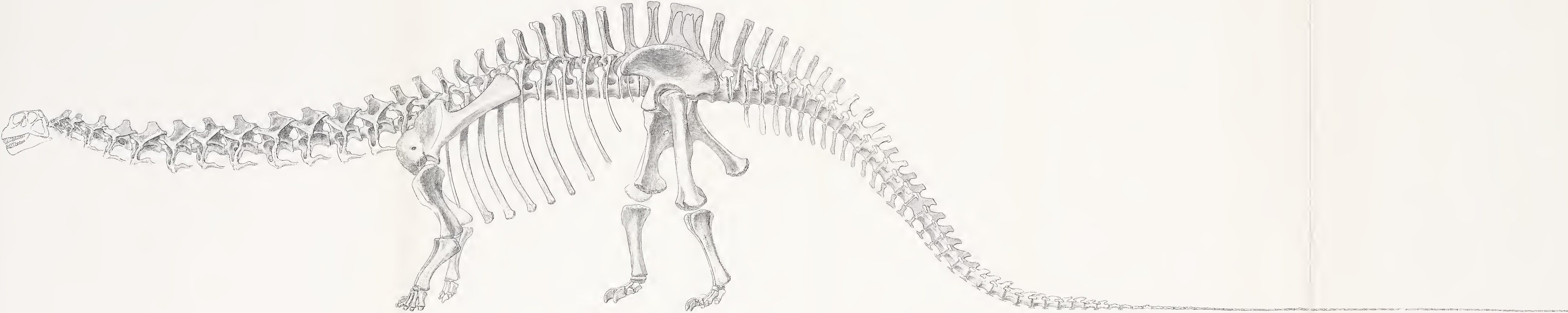
Restoration of the skeleton of *Apatosaurus louisæ* Holland. Based primarily on the mounted skeleton (No. 3018) in the Carnegie Museum. Drawn by Mr. Sydney Prentice. The skull is based upon a restored skull in the Carnegie Museum No. 12020, which may pertain to a large *Camarasaurus*.

One-thirtieth natural size.













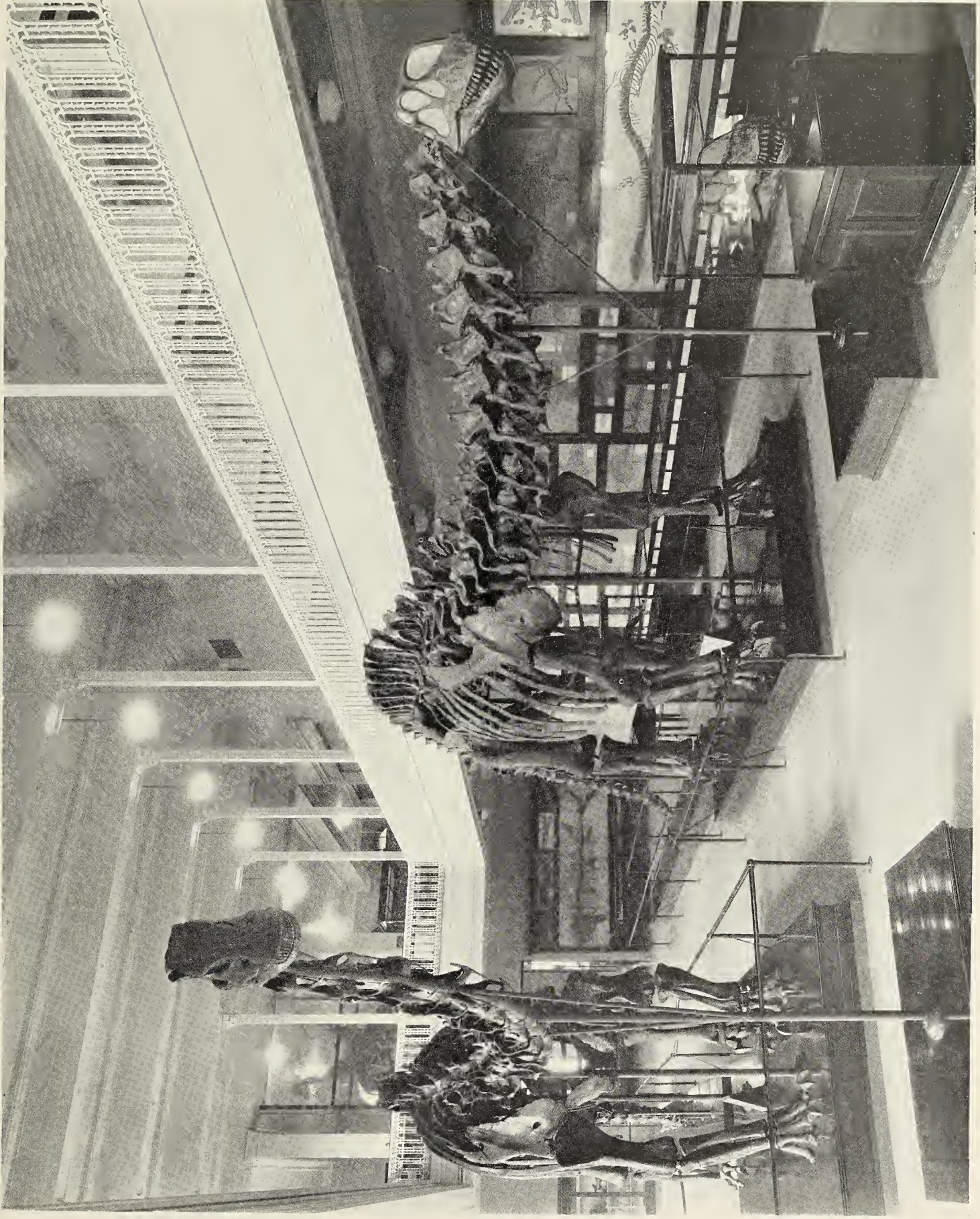




## EXPLANATION OF PLATE XXXV.

Mounted skeleton of *Apatosaurus louisæ* Holland, No. 3018, as exhibited in the Carnegie Museum.  
The mounted skeleton of *Diplodocus carnegii* shown on the left hand side.

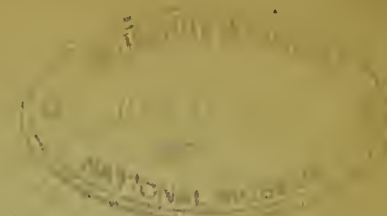








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MEMOIRS  
OF THE  
CARNEGIE MUSEUM

VOL. XI

ART. 5

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THE SOUTH AMERICAN TINGITIDÆ (HEMIPTERA)  
DESCRIBED BY STÅL.

By C. J. DRAKE AND M. E. POOR

PITTSBURGH  
PUBLISHED BY THE AUTHORITY OF THE BOARD OF TRUSTEES OF THE  
CARNEGIE INSTITUTE  
January 25, 1937





# MEMOIRS OF THE CARNEGIE MUSEUM

VOL. XI.

ART. 5.

## THE SOUTH AMERICAN TINGITIDÆ (HEMIPTERA) DESCRIBED BY STÅL.

BY C. J. DRAKE AND M. E. POOR

(PLATE XXXVI)

Carlos Stål described forty-six species of Tingitidæ from the Western Hemisphere, three of which have been placed in synonymy. In the Annals of the Carnegie Museum, XVI, 1926, pp. 375-380, pl. XXXIV, Drake treated those forms known to occur in North and Insular America.

The present paper deals with the South American Tingitidæ characterized by Stål. Through the auspices of the Carnegie Museum, the authors have been very fortunate in securing the services of Madam Thérèse Ekblom, a very competent artist, for making figures 1-11, inclusive, of Stål's types from South America in the Stockholm Museum. Figures 12-15 were made by Miss Margaret E. Poor. A number of Stål's types have also been figured by G. C. Champion in the Biologia Centrali-America and in the Transactions of the Entomological Society of London, 1898, pp. 55-64, pls. II and III. The writers have examined specimens of all the American tingitids described by Stål, except *Leptodictya dorni*, *L. lepida*, *L. fuscocincta*, *Leptopharsa furcata*, *L. marginella*, and *Stephanitis mitrata*.

### 1. *Monanthia monotropidia* (Stål)

*Monanthia (Physatocheila) monotropidia* Stål, Rio Hemip., I, 1860, p. 63. (Rio Janeiro, ♀, Mus. Holm. et Stål).

*Monanthia (Monanthia) monotropidia* Stål, Enum. Hemip., III, 1873, p. 133. (Rio Janeiro; Bogota; Mus. Holm.).

*Monanthia monotropidia* Champion, Biol. Centr.-Amer., Rhynch., II, 1898, p. 47, Pl. III, figs. 24, 24a, 24b.

Very common and widely distributed in Insular and Central America, Mexico, and the northern half of South America. Specimens have been examined from

JUN 15 1937



Haiti, Cuba, Jamaica, Mexico, Guatemala, Costa Rica, Honduras, Panama, Peru, and Brazil. Stål's types were taken at Rio Janeiro, Brazil. Breeds on *Cordia gerascanthus* and *Cordia* spp.

2. **Teleonemia triangularis** (Blanchard) (Plate XXXVI, fig. 14)

*Lacometopus albilaterus* Stål, Rio Hemip., I, 1860, p. 65 (Rio Janeiro, ♀; Mus. Holm.).

*Tingis* (*Americia*) *albilatera* Stål, Enum. Hemip., III, 1873, p. 131 (Rio Janeiro; Mus. Holm.).

*Tingis triangularis* Blanchard, in d'Orbigny, Voy. Amer., VI (2), 1843, p. 219, Pl. XXIX, fig. 10 (colored).

*Teleonemia triangularis* Champion, Biol. Centr.-Amer., Rhynch., II, 1898, p. 43 (footnote, on synonymy); Drake, Mem. Carn. Mus., IX, 1922, p. 359.

Recorded in the literature from Bolivia and Brazil. Specimens have been examined from these countries, also from Paraguay. One example, labeled "*Bolivie* (*Chiquitos*), *d'Orbigny*, 1834," probably represents one of Blanchard's types. Champion (1898, p. 43) states that Stål's type of *T. (America) albilatera* agrees perfectly with Blanchard's figure of *T. triangularis*. An example from São Paulo, Brazil, is figured.

This large and very distinct species belongs to the division of the genus *Teleonemia* Stål, which has the costal area broad and composed of more than one row of areolæ. The paranota are strongly reflexed and biseriate. In an example from Bahia, Brazil, the paranotum is uniseriate on one side and biseriate on the other. The costal area varies from four to six areolæ at its widest part. The areolæ are somewhat confused and not arranged in very regular rows. The spines on the head also exhibit some variation in size.

3. **Teleonemia limbata** (Stål)

*Tingis* (*Americia*) *limbata* Stål, Enum. Hemip., III, 1873, p. 131 (Bogota, Nova Granada; Rio Janeiro, ♂, ♀; Mus. Holm.).

*Teleonemia* (*Americia*) *limbata* Champion, Trans. Ent. Soc. Lond., 1898, p. 62, Pl. III, fig. 10.

Numerous specimens have been examined from Brazil and Paraguay. The type from Rio Janeiro, Brazil, has been figured by Champion.

Recognizable by the almost entirely biseriate costal area, strongly foliaceous carinæ, and the distinctly raised, roof-like anterior portion of the pronotum. The latter forms a hood-like structure and is slightly produced in front.

4. **Teleonemia morio** (Stål)

*Tropidocheila morio* Stål, Öfvers. af K. Vet. Acad. Förh., 1855, p. 187.

*Lacometopus morio* Stål, Rio Hemip., I, 1860, p. 65 (Rio Janeiro, ♂, ♀; Mus. Holm.).

*Teleonemia* (*Amaurosterphus*) *morio* Stål, Enum. Hemip., III, 1873, p. 131 (Rio Janeiro; Mus. Holm.).

*Teleonemia* (*Amaurosterphus*) *morio* Champion, Trans. Ent. Soc. Lond., 1898, p. 61, Pl. III, fig. 2.

Specimens are at hand from Rio Janeiro, Bahia, Chapada, Entre Rios, Brazil; and from Balén, Paraguay. Champion (1898, p. 61) figured Stål's type from Rio Janeiro. The uniseriate costal area, sub-globose hood and black color are distinguishing characters.

5. ***Teleonemia aterrima*** (Stål) (Plate XXXVI, fig. 15)

*Teleonemia* (*Teleonemia*) *aterrima* Stål, Enum. Hemip., III, 1873, p. 131 (Nova Granada, Bogota, ♂; Mus. Holm.).

*Teleonemia aterrima* Champion, Trans. Ent. Soc. Lond., 1898, p. 62, Pl. III, fig. 3.

Black species with uniseriate costal area. Specimens vary in size, length of antennæ and degree of elevation of hood-like anterior portion of pronotum. Several examples: Santarem, Brazil; Marcapata, Peru; and Colombia. Champion illustrated a specimen in the Oxford Museum from the Amazons. A specimen from Santarem, Brazil, is figured.

6. ***Teleonemia validicornis*** (Stål)

*Teleonemia* (*Teleonemia*) *validicornis* Stål, Enum. Hemip., III, 1873, p. 132 (Bogota, ♂; Mus. Holm.).

*Teleonemia validicornis* Champion, Trans. Ent. Soc. Lond., 1898, p. 62, Pl. III, fig. 4.

Very common and widely distributed: Para, Santarem, and Bahia, Brazil; Cayenne, French Guiana; Pernambuco, Mallali, British Guiana; and Paramaribo, Dutch Guiana. A long series of specimens from Bahia were taken upon the leaves of *Mucheria oblongifolium* V. *subglabrum* by Dr. Gregorio Bondar.

7. ***Teleonemia luctuosa*** (Stål)

*Lacometopus luctuosus* Stål, Rio Hemip., I, 1860, p. 65 (Rio Janeiro, ♂; Mus. Holm.).

*Teleonemia* (*Teleonemia*) *luctuosa* Stål, Enum. Hemip., III, 1873, p. 132 (Rio Janeiro; Mus. Holm.).

*Teleonemia luctuosa* Champion, Trans. Ent. Soc. Lond., 1898, p. 62, Pl. III, fig. 5.

Rare in collections. Two specimens from Rio Janeiro, Brazil, seem to agree with the original description and Champion's figure of the type. Known also from Paraguay. Median portion of pronotum in front broadly and only moderately elevated, faintly produced in front. Pronotum rugulose, shiny, coarsely pitted, the lateral carinæ distinctly constricted near the middle. Costal area very narrow, the areolæ narrow and long.



8. *Teleonemia proluxa* (Stål)

*Lacometopus proluxus* Stål, Rio Hemip., I, 1860, p. 65 (Rio Janeiro, ♂; Mus. Holm.).

*Teleonemia (Teleonemia) proluxa* Stål, Enum. Hemip., III, 1873, p. 132 (Rio Janeiro; Mus. Holm.).

*Acanthia sacchari* Fabricius, Ent. Syst., IV, 1794, p. 77.

*Monanthia (Tropidochila) sacchari* Stål, Stett. Ent. Zeit., 1862, p. 325.

*Teleonemia proluxa* Champion, Biol. Centr.-Amer., Rhynch., II, 1898, p. 39 (describes varieties  $\alpha$  and  $\beta$ ).

One of the commonest and most widely distributed members of the genus in South America. Many examples from Brazil, Paraguay, Peru, Argentina, Panama, British Guiana, and Colombia; also recorded from Central America and Mexico.

Very variable in size and color, and difficult to understand. Perhaps more than one species may be represented under the name *proluxa* Stål and the varieties as described by Champion.

9. *Teleonemia scrupulosa* (Stål)

*Teleonemia (Teleonemia) scrupulosa* Stål, Enum. Hemip., III, 1873, p. 132 (Rio Janeiro; Bogota, ♂, ♀; Mus. Holm.).

*Teleonemia scrupulosa* Champion, Biol. Centr.-Amer., Rhynch., II, 1898, p. 40, Pl. III, figs. 12 and 12a.

*Teleonemia lantanae* Distant, Entomologist, XL, 1907, p. 60.

*Teleonemia bifasciata* Distant (not Champion) Bull. Soc. Ent. France, No. 15, 1905, p. 216; Kirkaldy, Proc. Hawaiian Ent. Soc., I, 1908, p. 190.

*Teleonemia lantanae* Kirkaldy, Proc. Hawaiian Ent. Soc., I, 1907, p. 154, and 1908, pp. 182-190.

One of the commonest and the most widely distributed member of the genus *Teleonemia* in the Western Hemisphere—ranging from Texas and Florida south through the West Indies, Mexico, Central America, and into Colombia and Brazil. The long series of specimens includes three determined by Champion and one of Stål's cotypes from Bogota.

Breeds on mint, *Lantana* spp., and often found in abundance on this plant. Regarding this insect in Hawaii, Kirkaldy (1907, p. 154) states "This tingid was purposely introduced from Mexico to check the *Lantana camara* and has already succeeded to a wonderful degree."

10. *Amblystira pallipes* (Stål)

*Monanthia (Tropidocheila) pallipes* Stål, Rio Hemip., I, 1860, p. 62 (Rio Janeiro; Mus. Holm.).

*Amblystira pallipes* Stål, Enum. Hemip., III, 1873, p. 120 and 129 (Rio Janeiro; Mus. Holm.).

*Amblystira pallipes* Champion, Trans. Ent. Soc. Lond., 1898, p. 61, Pl. II, fig. 12.

Known heretofore only from the types, Rio Janeiro, Brazil. Two examples: Rio Frio, Colombia; Corumba, Matto Grosso, Brazil. *A. silvicola* Drake is a closely allied species. The latter differs in having the apical portion of the discoidal area acutely angulate and strongly raised at the apex; the costal area is also broader and much lighter in color at its widest part.

11. ***Sphærocysta inflata* (Stål) (Plate XXXVI, fig. 5)**

*Tingis* (?) *inflata* Stål, Rio Hemip., I, 1860, p. 64 (Rio Janeiro, ♀; Mus. Holm.).  
*Sphærocysta inflata* Stål, Enum. Hemip., III, 1873, p. 128 (Rio Janeiro; Mus. Holm.).

Described from specimens collected in Rio Janeiro, Brazil, and known only from there. The larger hood, broader costal area and much broader posterior portion of the paranota separate it from *globifera*. Six species of *Sphærocysta* have been described, all from Brazil. The type, Stockholm Museum, is figured.

12. ***Sphærocysta globifera* (Stål)**

*Tingis* (?) *globifera* Stål, Rio Hemip., I, 1860, p. 65 (Rio Janeiro, ♂, ♀; Mus. Holm. et Stål).  
*Sphærocysta globifera* Stål, Enum. Hemip., III, 1873, p. 128 (Rio Janeiro; Mus. Holm.).  
*Sphærocysta globifera* Champion, Trans. Ent. Soc. Lond., 1898, p. 61, Pl. II, fig. 11 and 11a.

Many specimens, all from Brazil. The very narrow, uniseriate paranota separate this insect at once from *S. stål*i Drake. In the latter the tumid elevations of the elytra and the inflated, apical portion of the median carina are larger. *Globifera* is the logotype of the genus *Sphærocysta* Stål.

13. ***Tigava præcellens* (Stål)**

*Tigava præcellens* Stål, Rio Hemip., I, 1860, p. 63 (Rio Janeiro, ♀; Mus. Holm.).  
*Tigava præcellens* Stål, Enum. Hemip., III, 1873, p. 121 and 130 (Rio Janeiro; Mus. Holm.).  
*Tigava præcellens* Champion, Trans. Ent. Soc. Lond., 1898, p. 61, Pl. III, fig. 1.

The genus *Tigava* was founded by Stål for *præcellens* from Rio Janeiro, Brazil. Several specimens are at hand from Chápada and Corumba (Matto Grosso), Brazil; and one from Cochabamba, Bolivia. The broader costal area and paranota, the more prominent carinæ, and slightly smaller size separate *præcellens* from *convexicollis* Champ. In addition to the above species, the genus contains *T. semota* Drake, *nobilis* Drake, and *cassiæ* Drake and Hambleton. Several other species described as *Tigava* have been recently transferred to the genus *Campylotingis* Drake.



14. *Acanthochila armigera* (Stål)

*Monanthia* (*Acanthocheila*) *armigera* Stål, Rio Hemip., I, 1860, p. 61 (Rio Janeiro, ♂, ♀; Mus. Holm. et Stål).

*Acanthochila armigera* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

*Monanthia spinuligera* Stål, Rio Hemip., I, 1860, p. 61.

*Acanthochila spinuligera* Stål, Enum. Hemip., III, 1873, p. 127.

*Acanthocheila armigera* Champion, Biol. Centr.-Amer., Rhynch., II, 1897, p. 28, Pl. II, figs. 19 and 19a.

Widely distributed; specimens have been examined from Brazil, Peru, Bolivia, Colombia, Panama, Nicaragua, Honduras, Porto Rico, Cuba, Jamaica, Haiti, and Trinidad. Recently the writers have received a series of specimens from Brownsville, Texas, collected by J. M. Knull. Very variable in size, ranging from 3.00 to 5.50 mm. in length. Marginal spines of paranota and elytra are also variable in number and length.

15. *Leptocysta sexnebulosa* (Stål) (Plate XXXVI, fig. 13)

*Tingis sex-nebulosa* Stål, Rio Hemip., I, 1860, p. 64 (Rio Janeiro, ♂; Mus. Holm.).

*Leptocysta sexnebulosa* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

*Leptocysta sexnebulosa* Champion, Trans. Ent. Soc. Lond., 1898, p. 61, Pl. II, figs. 10 and 10a.

Known from Argentina, Brazil, Paraguay, and Colombia. *L. novatis* Drake from Argentina, the only other member of the genus, may readily be distinguished from it by the much less swollen and shorter pronotum and by the very short lateral carinae, which strongly divaricate posteriorly. A specimen from Brazil is figured.

16. *Leptodictya ochropa* (Stål) (Plate XXXVI, fig. 4)

*Monanthia* (*Physatocheila*) *ochropa* Stål, Rio Hemip., I, 1860, p. 62 (Rio Janeiro, ♂; Mus. Holm.).

*Leptodictya ochropa* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

Size and color quite variable, especially color of costal area. The color of the broad marginal border of elytra varies from brown to very dark fuscous; costal margin closely and finely serrate.

In Boletim do Museu Nacional, Vol. VII, No. 2, 1931, pp. 119-122, Drake divides the genus *Leptodictya* Stål into the subgenus *Leptodictya* Drake (type = *ochropa* Stål) and *Hanuala* Kirkaldy (type = *leinahoni* Kirkaldy). In *ochropa* (only member of subgenus *Leptodictya*) the paranota are completely reflexed from the base and conform to and rest entirely upon the upper surface of the pronotum.

Known only from Brazil; specimens from Bahia, São Paulo, and Diamantina have been examined. Stål's type in the Stockholm Museum is figured.

17. **Leptodictya approximata** (Stål) (Plate XXXVI, fig. 3)

*Monanthia (Physatocheila) approximata* Stål, Rio Hemip., I, 1860, p. 63 (Rio Janeiro; Mus. Holm.).

*Leptodictya approximata* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

Two examples: São Paulo, Brazil and Blairmont, British Guiana. Stål's type from Rio Janeiro is figured. Carinæ foliaceous, each uniseriate. Head brown, with five long, slender, testaceous spines.

18. **Leptodictya fuscocincta** (Stål)

*Monanthia (Physatocheila) fusco-cincta* Stål, Rio Hemip., I, 1860, p. 62 (Rio Janeiro, ♀; Mus. Holm. et Stål).

*Leptodictya fusco-cincta* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

Known only from specimens in the Stockholm Museum. Stål's type from Rio Janeiro has been figured by Champion.

19. **Leptodictya dohrni** (Stål) (Plate XXXVI, fig. 1)

*Monanthia (Physatocheila) dohrnii* Stål, Rio Hemip., I, 1860, p. 62 (Rio Janeiro, ♀; Mus. Holm.).

*Leptodictya dohrnii* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

Known only from the type locality and a series of specimens from Tambo Euenas, Peru. Stål's type from Rio Janeiro is figured.

20. **Leptodictya lepida** (Stål) (Plate XXXVI, fig. 2)

*Monanthia (Physatocheila) lepida* Stål, Rio Hemip., I, 1860, p. 63 (Rio Janeiro; Mus. Stål).

*Leptodictya lepida* Stål, Enum. Hemip., III, 1873, p. 127 (Rio Janeiro; Mus. Holm.).

Known only from the type locality, Rio Janeiro, Brazil. Stål's type is figured.

21. **Leptopharsa vittipennis** (Stål) (Plate XXXVI, fig. 11)

*Leptostyla vittipennis* Stål, Enum. Hemip., III, 1873, p. 126 (Rio Janeiro, ♂; Mus. Holm.).

One specimen, Vilcanota, Peru. Stål's type from Rio Janeiro, Brazil, is figured. Resembles *L. furculata* Champion in color and general appearance, but longer, with wider costal area, and fuscous-black basal segment of antennæ.



22. *Leptopharsa furcata* (Stål) (Plate XXXVI, fig. 7)

*Leptostyla furcata* Stål, Enum. Hemip., III, 1873, p. 126 (Rio Janeiro, ♂, ♀; Mus. Holm.).

*Leptostyla furcata* Champion, Trans. Ent. Soc. Lond., 1898, p. 60, Pl. II, figs. 7, 7a.

Known only from type specimen. The type is figured.

23. *Leptopharsa hyaloptera* (Stål)

*Leptostyla hyaloptera* Stål, Enum. Hemip., III, 1873, p. 126 (Rio Janeiro, ♂, ♀; Mus. Holm.).

Head brown, shiny, tumid above; median spine short, blunt, porrect; posterior spines short, resting upon surface of head; frontal spines very short. Spines, paranota and carinæ testaceous. Antennæ long, yellowish brown; segment I rather stout, three times as long as II. Bucculæ testaceous, closed in front. Rostral channel open behind, the laminæ widely separated on mesosternum, the rostrum extending almost to end of mesosternum. Pronotum moderately tumid, distinctly pitted, dark reddish brown, tricarinate; lateral carinæ foliaceous, practically parallel, uniseriate, the areolæ small; median carina slightly more elevated. Hood moderately large, slightly projecting anteriorly. Elytra, wings, and last segment of antennæ wanting in this specimen. Legs testaceous, long, slender.

The above notes were taken from Stål's type in the Stockholm Museum. *Leptopharsa ignota* D. & H. is a closely allied species. The latter has a slightly larger hood, the lateral carinæ slightly converging posteriorly and the paranota bi-triseriate. *Hyaloptera* is known only from the type specimens.

24. *Leptopharsa elegantula* Stål

*Leptopharsa elegantula* Stål, Enum. Hemip., III, 1873, p. 126 (Bogota, Nova Granada, ♂; Mus. Holm.).

*Leptopharsa elegantula* Champion, Trans. Ent. Soc. Lond., 1898, p. 60, Pl. II, fig. 8.

Four examples, Cochabamba, Bolivia; type from Rio Janeiro has been figured by Champion. Pronotum tricarinate; each carina indistinctly areolate. Costal area whitish testaceous, mostly biseriate, irregularly triseriate at widest part. Paranota biseriate, the areolæ (also of costal area) transparent and somewhat iridescent.

A closely allied species, *Leptoharsa distantis* Drake, from Mexico and Haiti may be separated from *elegantula* by its smaller size, less elevated carinæ, and the elevated anterior portion of the median carina; the discoidal area is also shorter and broader at apex.

25. **Leptopharsa marginella** (Stål) (Plate XXXVI, fig. 6)

*Monanthia* (*Tropidocheila*) *marginella* Stål, Rio Hemip., I, 1860, p. 62 (Rio Janeiro; Mus. Holm.).

*Leptopharsa marginella* Stål, Enum. Hemip., III, 1873, p. 126 (Rio Janeiro; Mus. Holm.).

Known only from the type, which is figured. The very narrow paranota and lateral carinæ are quite distinctive. The structure of the pronotum, lateral carinæ, and head seem to indicate that *marginella* may not be very typical of the genus *Leptopharsa*.

26. **Stephanitis mitrata** (Stål)

*Tingis mitrata* Stål, Rio Hemip., I, 1860, p. 64 (Rio Janeiro, ♀; Mus. Holm.).

*Stephanitis mitrata* Stål, Enum. Hemip., III, 1873, p. 123 (Rio Janeiro; Mus. Holm.).

*Stephanitis mitrata* Champion, Trans. Ent. Soc. Lond., 1898, p. 58, Pl. II, fig. 3, 3a.

Known only from Rio Janeiro, Brazil, the type locality. Champion has published an excellent figure of Stål's type.

27. **Leptobyrsa steini** (Stål)

*Tingis steini* Stål, Rio Hemip., I, 1860, p. 64 (Rio Janeiro, ♂; Mus. Holm. et Stål).

*Leptobyrsa steinii* Stål, Enum. Hemip., III, 1873, p. 123 (Rio Janeiro; Mus. Holm.).

*Leptobyrsa steini* Champion, Trans. Ent. Soc. Lond., 1898, p. 58, Pl. II, fig. 4.

Determination of this species is based upon a cotype from Rio Janeiro, Brazil. It also agrees with Champion's figure of Stål's type. Several specimens from Brazil have been examined.

28. **Gargaphia flexuosa** (Stål) (Plate XXXVI, fig. 10)

*Monanthia flexuosa* Stål, Rio Hemip., I, 1860, p. 61 (Rio Janeiro, ♀; Mus. Holm.).

*Gargaphia flexuosa* Stål, Enum. Hemip., III, 1873, p. 124 (Rio Janeiro; Mus. Holm.).

Known only from Rio Janeiro, Brazil. The type is figured.

29. **Gargaphia patricia** (Stål)

*Monanthia* (*Phyllontochila*) *patricia* Stål, Stett. Ent. Zeit, XXIII, 1862, p. 324 (Mexico; Mus. Holm.).

*Gargaphia patricia* Stål, Enum. Hemip., III, 1873, p. 125 (Mexico; Mus. Holm.).

*Gargaphia patricia* Champion, Biol. Centr.-Amer., Rhynch., II, 1897, p. 9, Pl. I, fig. 12, 12a.

*Gargaphia patricia* Drake, Ann. Carn. Mus., XVI, 1926, p. 377.

Very common in Mexico and Central America. Many other specimens are at hand from the West Indies, Colombia, and Argentina.



30. *Gargaphia obliqua* Stål, (Plate XXXVI, fig. 9)

*Gargaphia obliqua* Stål, Enum. Hemip., III, 1873, p. 124 (Rio Janeiro, ♂; Mus. Holm.).

Many examples, Rio Janeiro, Chapada, Vicosá, and Pedro Leopoldo, Brazil. Feeds on *Serjania* spp. Stål's type is figured.

31. *Gargaphia formosa* (Stål)

*Monanthia* (*Phyllontocheila*) *formosa* Stål, Rio Hemip., I, 1860, p. 61 (Rio Janeiro, ♀; Mus. Holm. et Stål).

*Gargaphia formosa* Stål, Enum. Hemip., III, 1873, p. 125 (Rio Janeiro; Mus. Holm.).  
*Tingis formosa* Göldi, Mitth. Schweiz. Ent. Ges., VIII, 1886, pp. 234 and 241.

One specimen, Rio Janeiro, Brazil, and known only from there. Costal area broad, with a broad, transverse, black-fuscous band (formed by colored nervures) a little in front of the middle, the areolæ rather large, somewhat variable in size, not arranged in very regular rows, six cells at widest part; subcostal area triseriate; discoidal area narrow, short, impressed, most of nervelets black-fuscous, composed of four rows of areolæ at widest part. Paranota broad, strongly reflexed, widest opposite humeri, there four areolæ deep. Pronotum black, tricarinate, each carina composed of a single row of moderately large cells; the median carina more strongly raised. Antennæ long, pilose; segments I and II dark brown, the first constricted near apex, considerably thicker and three times as long as the second; III testaceous, two and one-half times as long as IV, the latter long and blackish.

32. *Gargaphia munda* (Stål) (Plate XXXVI, fig. 12)

*Monanthia* (*Phyllontocheila*) *munda* Stål, Rio Hemip., I, 1860, p. 60 (Rio Janeiro, ♀; Mus. Holm. and Stål).

*Gargaphia munda* Stål, Enum. Hemip., III, 1873, p. 124 (Rio Janeiro; Mus. Holm.).

*Monanthia lineifera* Walker, Cat. Hemip., VI, 1873, p. 194 (Brazil).

*Gargaphia magna* Gibson, Trans. Amer. Ent. Soc., XLV, 1919, p. 194.

*Gargaphia munda* Drake, Bull. Ent. Soc. Fla., V, 1922, p. 41.

Common and quite generally distributed in Brazil and Peru. Breeds upon *Brunfettisia* sp. and *Solanum* spp. (Solanaceæ). *G. magna* Gibson (type, U. S. N. M.) is a synonym of *G. munda* Stål.

33. *Gargaphia simulans* (Stål) (Plate XXXVI, fig. 8)

*Monanthia* (*Phyllontocheila*) *simulans* Stål, Rio Hemip., I, 1860, p. 61 (Rio Janeiro, ♀; Mus. Holm.).

*Gargaphia simulans* Stål, Enum. Hemip., III, 1873, p. 124 (Rio Janeiro; Mus. Holm.).

Known only from Rio Janeiro, Brazil. Stål's type is figured.

34. *Gargaphia trichoptera* Stål

*Gargaphia trichoptera* Stål, Enum. Hemip., III, 1873, p. 125 (Bogota, Nova Granada, ♂, ♀; Mus. Holm.).

*Gargaphia trichoptera* Champion, Trans. Ent. Soc. Lond., 1898, p. 58, Pl. II, fig. 5.

Antennæ long, rather densely clothed with long, fine hairs, brownish testaceous, the apical segment black; segment I thicker and two and one-half times as long as II; III three times as long as IV. Head brown, tumid above, with fine, long, sharp, slender, testaceous spines, the median longest and porrect. Hood testaceous, rather small, compressed laterally, faintly produced in front. Pronotum tricarinate, black, the triangular portion testaceous; carinæ strongly foliaceous, each uniseriate, the areolæ moderately large. Paranota broad, strongly reflexed, testaceous, the lateral margin finely serrate; costal area very broad, with five or six enlarged, oblique, brown to fuscous nervures, the areolæ moderately large, slightly variable in size and not arranged in regular rows; subcostal area mostly biseriate; discoidal area long, broad, narrowed at both base and apex, widest slightly beyond the middle, there six or seven areolæ deep. Nervures sparsely clothed with long, very fine hairs.

The above notes were taken from a male, cotype, Bogota, Colombia; not known from elsewhere. Champion has published an excellent figure of Stål's type.

35. *Gargaphia nigrinervis* Stål

*Gargaphia nigrinervis* Stål, Enum. Hemip., III, 1873, p. 125 (Bogota, ♂; Mus. Holm.).

*Gargaphia nigrinervis* Champion, Biol. Centr.-Amer., Rhynch., vol. II, 1897, p. 10, Pl. I, figs. 13, 13a.

Very common and widely distributed in Colombia and Panama. The smaller size and angulate paranota separate it from *G. trichoptera* Stål.

36. *Corythaica monacha* (Stål)

*Tingis monacha* Stål, Rio Hemip., I, 1860, p. 64 (Rio Janeiro, ♂, ♀; Mus. Holm. and Stål).

*Corythaica monacha* Stål, Enum. Hemip., III, 1873, p. 128 (Rio Janeiro; Mus. Holm.).

*Corythaica monacha* Drake and Bruner, Mem. Soc. Cuba Hist. Nat., VI, 1924, p. 151.

The members of the genus *Corythaica* have been greatly confused in the literature. Drake and Bruner (1924, p. 151) pointed out the differences between *C. monacha* Stål and *C. planaris* Uhler. The two species are quite distinct and not easily confused.

*C. planaris* Uhler: larger, thicker veins and more widely reticulated; hood larger, somewhat flattened behind; median carina not distinctly arched, almost entirely uniseriate, slightly more elevated than lateral ones; discoidal area impressed along the inner margin and distinctly elevated towards subcostal margin; subcostal area bi- to triseriate; costal area largely biseriate, the areolæ not arranged in regular rows, the transverse fascia very distinct to almost entirely wanting.



*Planaris* is very common in the West Indies and South America and feeds upon *Solanum* spp. It is a pest of considerable importance of the cultivated egg plant. Under the name of *monacha* (= *planaris* Uhl.), Cotton, Journ. Dept. Agr., Porto Rico, I, 1917, pp. 170-173, published on its habits and life history. Most of the records of *C. monacha* (not Stål) from the West Indies should be referred to *planaris* Uhler. The writers' determination of *planaris* is based upon one of Uhler's cotypes from the British Museum. The color is quite variable, and the median carina is more elevated in some specimens than in others.

*C. monacha* Stål: smaller than *planaris*; hood narrower, inflated behind; median carina strongly arched, there biseriate. Elytra with large tumid elevation, which is formed by the elevation of boundary between subcostal and discoidal areas; discoidal area not impressed, its entire surface sloping towards sutural area, not bounded by prominent nervures.

Known from Brazil, Argentina, and Chile. The determination is based upon one of Stål's cotypes. The size, hood, median carina and discoidal area furnish good characters for the separation of this species from *planaris* Uhl.

### 37. *Corythucha fuscomaculata* (Stål)

*Tingis fusco-maculata* Stål, Rio Hemip., I, 1860, p. 63 (Rio Janeiro, ♂, ♀; Mus. Holm. and Stål).

*Corythucha fusco-maculata* Stål, Enum. Hemip., III, 1873, p. 123 (Rio Janeiro; Nova Granada; Mus. Holm.).

*Corythucha fuscomaculata* Champion, Trans. Ent. Soc. Lond., 1898, p. 57, Pl. II, fig. 2.

Found abundantly in Brazil and Peru; the commonest member of the genus *Corythucha* in South America.

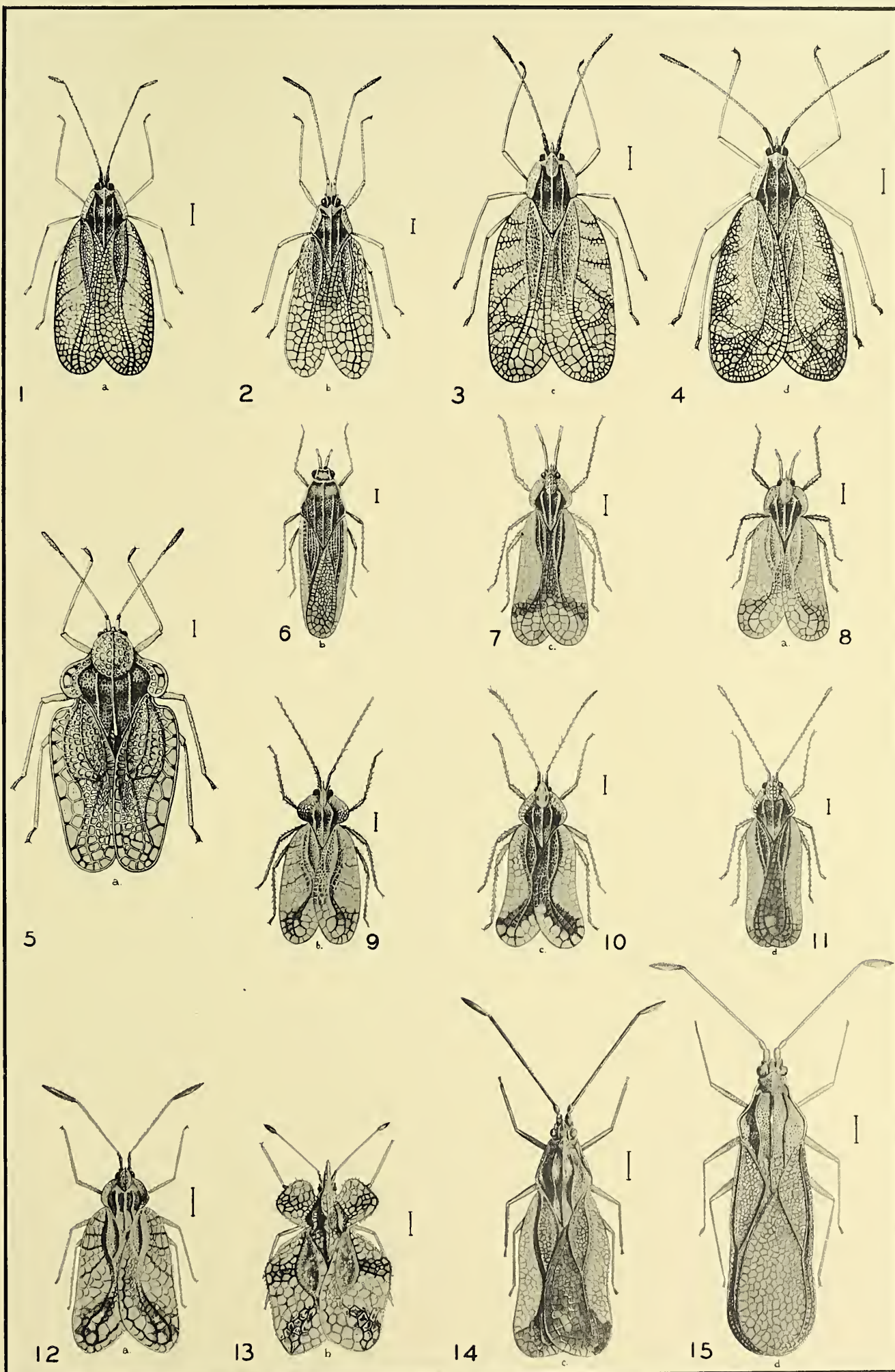




## EXPLANATION OF PLATE XXXVI

Figures 1 to 11 are by Thérèse Ekblom; figures 12 to 15 by Margaret E. Poor.

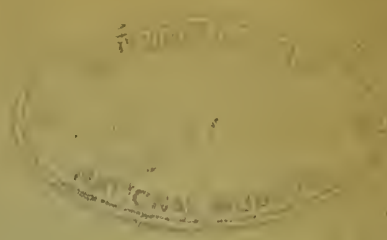
- FIG. 1. *Leptodictya dohrni* (Stål).
- FIG. 2. *Leptodictya lepida* (Stål).
- FIG. 3. *Leptodictya approximata* (Stål).
- FIG. 4. *Leptodictya ochropa* (Stål).
- FIG. 5. *Sphærocysta inflata* (Stål).
- FIG. 6. *Leptopharsa marginella* (Stål).
- FIG. 7. *Leptopharsa (Leptostyla) furcata* (Stål).
- FIG. 8. *Gargaphia simulans* (Stål).
- FIG. 9. *Gargaphia obliqua* Stål.
- FIG. 10. *Gargaphia (Monanthia) flexuosa* (Stål).
- FIG. 11. *Leptopharsa (Leptostyla) vittipennis* (Stål).
- FIG. 12. *Gargaphia munda* (Stål).
- FIG. 13. *Leptocysta sexnebulosa* (Stål).
- FIG. 14. *Teleonemia (Tingis) triangularis* (Blanchard).
- FIG. 15. *Teleonemia aterrima* (Stål).







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MEMOIRS  
OF THE  
CARNEGIE MUSEUM

VOL. XI

ART. 6

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A CATALOGUE OF  
THE SPANG COLLECTION OF GREEK AND ITALIAN VASES AND  
ETRUSCAN URNS IN THE CARNEGIE MUSEUM

By HENRY S. SCRIBNER  
Professor Emeritus of Greek, University of Pittsburgh

(PLATES XXXVII-XLIII)

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## A CATALOGUE OF THE SPANG COLLECTION OF GREEK AND ITALIAN VASES AND ETRUSCAN URNS IN THE CARNEGIE MUSEUM

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## INTRODUCTION

The Spang Collection of Greek and Italian Vases and Etruscan Urns was purchased in 1853 at Chiusi (Latin Clusium), Italy, by Mr. Charles Frederick Spang, who requested that the collection be donated to the first museum to be established in Pittsburgh.

Mr. Spang, who was one of the founders of the Pittsburgh firm of Spang, Chalfant and Company, died in Nice, France, on July 18, 1904, in the ninety-fifth years of his age. His collection has for many years been housed in the Carnegie Museum.

Miss Rosalie Spang, the daughter of Charles Frederick Spang, died in Nice, on April 15, 1932, and by her will the collection was left to the Carnegie Museum.

After a long search and diligent inquiry the author of this Catalogue has been unable to find any records or letters of Mr. Spang which might throw light on the circumstances of the acquisition of the vases. Such details would include the names of persons from whom they were bought and their supposed provenance. There is a tradition that they came from Chiusi, and this tradition I have followed.

The vases and urns have never been catalogued or published upon before, and should be the nucleus for future additions to this important field of ancient art.

In preparing this catalogue I have been greatly indebted for help and valuable suggestions to Dr. David M. Robinson, Vickers Professor of Archaeology, of Johns Hopkins University. He supplied me with many references and corrected many errors. This acknowledgment of his assistance will, I hope, show my appreciation of his aid in many matters in which I was in doubt.

I am also sincerely grateful to Dr. Eva Fiesel, visiting professor of linguistics at Bryn Mawr College, for her kindness in sending me the transcriptions and interpretations of the Etruscan inscriptions on the urns which are illustrated on plate XLIII, figures 3 and 4.

To Mr. Sydney Prentice, my thanks are due for his patience and skill in preparing the photographs.

JUN 15 1937

## GREEK AND ITALIAN VASES

## DESCRIPTIONS OF THE INDIVIDUAL VASES

**Black-figured Column Krater or Kelebe.** Plate XXXVII, Obverse;  
Pl. XXXVIII, Reverse.

Height .336 m., diameter .305 m.

Obverse (plate XXXVII); a narrow reserved band is at the base of the molded foot; next there are up-pointing rays beneath a broad black band, on which rest the two painted panels, each of which is enclosed on the sides by a double row of ivy leaves within lines, and, above the shoulders, by a tongue pattern. The wide, almost vertical neck supports the overhanging rim which is decorated with a double row of rudely drawn ivy leaves separated by a narrow black line.

On the exterior surface of the lip, there is a frieze of lotus buds with intersecting stems, and on the flat projections over the columnar handles, a palmette. The double handles rise in an arch almost vertically from the shoulders. The black glaze is somewhat worn off on the neck, handles, and foot.

The body of the vase is somewhat ovoid, rounding sharply on the shoulder.

Two warriors, probably Achilles and Ajax, are seated on cylindrical stools playing a board-game, probably "draughts," at a low table between them. Each of the players wears a *taenia* about his hair, a chiton with a purple border, which appears below his cuirass, and greaves.

The chitons are decorated with purple dots and incised stars. The warriors wear on their legs thigh-pieces or perimeridia. Both the cuirasses and the perimeridia have spiral ornaments. Each warrior holds two spears over his left shoulder. Both warriors have white beards, at least they appear white on the vases. Their eyes are in front view. They are absorbed in the game. Their shields and helmets lean against the wall behind them and the shields have circular indentations on each side, each being decorated with three white, solid circles and three purple dots near the edge. From the Corinthian helmets rise the lofty crests of three parts: a narrow, metal, curved piece, projecting from the top of the helmet; next, a flat curved piece, ornamented with white dots, and an outer, wider band, originally white, ending below in a long streamer.

In the rear, between the warriors, stands the goddess, Athena, her body to the front, her head inclined to the left, gazing at the left warrior, as if favoring him. In her right hand she holds her spear horizontally across her body and over the heads of the players. The goddess is clad in a close-fitting, sleeveless chiton with vertical, incised lines which extend in front from the waist two-thirds of the way to the ground; the chiton has an ornamental border. On the front of the



garment in the middle are three incised dots or stars, reaching to the hands of the players. The goddess wears her *aegis*, without the Medusa head, and an Attic helmet whose high crest is shortened and projects into the tongue pattern on the shoulder of the vase. The ear-flap of the helmet is down and there is a sort of covering from the back of the helmet to the left shoulder, from which hangs a fillet or streamer extending over her chest to her spear. The color of the face, neck, and arms of the goddess was originally white. The drawing of the figures is archaic, but vigorous and life-like. The upraised left arm lacks the hand, probably due to the curve of the shoulder of the vase.

Reverse (plate XXXVIII); four nude figures; in the center stand two dancing youths, back to back, their heads facing each other. On the left is a trainer, with his left hand raised, who is evidently giving instructions to the youth who is bending his body back toward his comrade, who raises his left foot in a less violent gesture and looks backward. At the extreme right stands another trainer holding a short stick in his right hand. Probably all four men are dancing.

The drawing is inferior to that on the obverse. Incised lines are sparingly employed. The muscles are exaggerated, and the elongation of the hands and feet, though a mark of archaic art, may be to some extent due to the carelessness of the painter.

Attic, about 530-520 B. C., Chiusi.

Representations on Greek vases of warriors playing at draughts are numerous. The names usually assigned are those of Achilles and Ajax.

*Cf.* Pfuhl, Ernst, Masterpieces of Greek Drawing and Painting, Beazley's translation, pp. 26-28, figs. 21-22; Furtwängler-Reichhold-Hauser, Griechische Vasen Malerei, Vol. III, p. 65 f., pls. 131-132; Hoppin, James Clark, Handbook of Attic Black-figure Vases, pp. 106-107; Walters, H. B., Catalogue of the Greek and Etruscan Vases in the British Museum, Vol. II, Black-figure Vases: B 193 Amphora (a), B 211 Amphora (a), B 438 Kylix (a), B 466 Kyathos, B 501 Oenochoe.

I have not been able to locate any other krater on which the scene of Achilles and Ajax playing draughts is depicted.

Professor J. D. Beazley of Oxford University, to whom I sent a photograph of the vase, wrote me that he could not assign the vase to any particular painter, nor could he see any trace of the influence of Exekias on the vase.

The story depicted on our vase is not found in Greek literature. The origin of the story may have been a poem or a painting that was reconstructed by the vase painters. Some commentators on the passage in Euripides, Iphigeneia in Aulis, 192 f., provisionally name the players Protesilaus, and Palamedes, the reputed inventor of the game of draughts, who were amusing themselves during the long



hours at Troy by playing a game. The illustrations on the vases, however, and the famous amphora by Exekias in the Vatican, Museo Gregoriano, on which the names of the two warriors are inscribed, make it probable that Achilles and Ajax are the names to be assigned to the players on our vase.

**Black-figured Eye Kylix.** Satyrs and Mænads. Plate XXXIX, figs. 1a, 1b.

Height .082 m., diameter .227m.

The cup has been repaired but no parts are missing. Decoration; black, red, and white on the light red color of the clay. Low, cylindrical foot; above is a reserved band.

Exterior (fig. 1a); a dionysiac scene, Satyrs and mænads. Four figures are depicted. On the left a satyr stands, facing right. In front of him is a large conventional eye, painted in white and red circular bands. The satyr looks in trepidation toward the two central figures, a satyr, advancing to the right in attacking pose toward a mænad, who advances toward him. The mænad holds in each hand a short drinking horn, and appears to be dancing. Her face, arms, and feet are painted white. The folds of her garments are red, marked with incised, white lines. On the right, behind a similar eye, another satyr looks back as he hastily retreats to the right. The hair, and the beards and tails of the satyrs are painted red. On three sides, a vine-branch pattern encompasses the central group and the eyes. Below one handle there is a flying bird, below the other is a figure which seems also to be a bird, but perhaps these figures do not represent birds.

For the meaning of the eye on Greek vases, *cf.* Dennis, G., *Cities and Cemeteries of Etruria*, Vol. I, p. 471; Walters, H. B., *History of Ancient Pottery*, Vol. I, pp. 357, 410, 427; W. Klein, *Euphronios*, p. 289, where, in his first classification of red-figure cups, he also includes black-figure kylikes with eyes, and Gorgon heads. For eye cups with gorgoneia, *cf.* *Corpus Vasorum Antiquorum*, Great Britain, Brit. Mus., Fasc., 2, III, He Pl. 19, 1a, 1b, and 1c, 2a, 2b, and 2c.

Reverse of exterior; the scene varies slightly from that on the obverse. On the left a satyr stands and gazes to the right at an object held up in his left hand. In the central group, stands a satyr, with hands down, gazing at a mænad, who turns back, apparently listening to his words. At the extreme right, a mænad retreats and looks back at the central figures.

Interior (fig. 1b); a gorgoneion within a medallion, grotesque, red, with red horns and misshapen ears. In front of a row of white tusks a large, red tongue hangs down. Below the tongue there is a row of incised, curved lines, perhaps meant for hair.

Attica, Early Sixth Century B.C.

On the interior of kylikes the gorgoneion is common. Cf. Robinson, Harcum, and Iliffe, Catalogue of Greek Vases in the Museum in Toronto, Nos. 291-292, pp. 105-106, and references cited there; Pfuhl, E., *Malerei und Zeichnung Der Griechen*, Vol. III, p. 15, Korinthisch orientalisierend (107 ff.).

The purpose of the gorgoneion was doubtless to serve as a charm to avert evil or bad luck.

#### THE GORGONEION.

The gorgoneion is mentioned in Homer, *Iliad*, V. 738 ff., on the ægis of Athena; *Iliad*, XI, 36 on the shield of Agamemnon; *Iliad* VIII, 349 in a comparison; and as a fearsome thing, in the *Odyssey*, XI, 634. See Professor Clark Hopkins, Yale University, *American Journal of Archaeology*, Vol. XXXVIII, p. 341, 1934.

Professor George H. Chase of Harvard University in his exhaustive article, "Shield Devices of the Greeks," *Harvard Studies in Classical Philology*, Vol. XIII, 1902, p. 61 ff., shows how common was the device of the gorgoneion on Attic shields which are depicted on vases. The vase painters imitated the actual designs painted or drawn on shields.

The Gorgon's head became one of the official coats-of-arms of the city of Athens.

Chase, *op. cit.*, pp. 106-107, CXIX, cites examples of this device on Attic vases, and on other monuments of the historic period, such as coins, sarcophagi, cistæ, marble and terra-cotta reliefs, temples, and city gates.

For a full discussion of the subject, see Furtwängler's article, *Gorgons*, in Roscher, *Lexikon der Griechischen und Römischen Mythologie*, I<sup>2</sup>, 1701 ff.

Mr. Humphry Payne, *Necrocorinthia*, Oxford, 1931, pp. 79-89, in discussing a series of gorgons and gorgoneia does not agree with Furtwängler as regards the Ionic origin of this device, but shows that the gorgon design originated in Corinth. Payne says (*op. cit.*, p. 89), "The principal tradition originated in Corinth and passed to Attica; from about the middle of the sixth century an Attic or Atticizing type became common property in the Ægean area." And again—"The gorgoneion was an atropaic symbol and it was early used as a decoration on Corinthian temples, and wherever Corinthian influence was felt."

For the gorgoneion as an architectural decoration, cf. Payne, *op. cit.*, p. 251 f. See also Payne, *op. cit.*, p. 83, fig. 25 A, and p. 87, fig. 27 C, where there is a close resemblance to the gorgoneion depicted on our cup.

Professor Robinson writes me that "in the Walters Art Gallery in Baltimore, there is a beautiful early Attic pinax with a gorgoneion in the center and animals round about it, showing Corinthian influence."



**Aryballos.** Plate XXXIX, fig. 2.

Height .053 m., maximum circumference .146 m.

The vase is of gray clay. There are three reserved bands on the shoulder, and dark bars on the surface of the convex top. The body of the vase was perhaps painted black, but the paint is worn off and no design can be distinguished. The neck is short, and a handle joins the lip and shoulder. The bottom of the vase is flat. Very rude work.

Italic-Corinthian, perhaps of the Sixth Century B.C.

For type, *cf.* Payne, *Necrocorinthia*, p. 321, fig. 162.

**Alabastron.** Plate XXXIX, fig. 3.

Height .095 m., maximum circumference .178 m.

Material, pinkish clay. The body of the vase is pear-shaped. There are five brown bands about the body and brown rays pointing up to the small narrow neck. The edge of the rim is slightly extended. The lip is flat and on its inner surface there is a brown circular band. A short, flat handle extends from the edge of the lip to the top of the shoulder.

Etruscan or Italian imitation of a Corinthian alabastron.

Early Sixth Century B.C.

*Cf.* Walters, *Cat. of Vases*, Brit. Mus., Part II, pl. IV, C, 774; J. L. Myres and M. Ohnefalsch-Richter, *Cat. of the Cyprus Museum*, 1023, 1062; Robinson, Harcum and Iliffe, *Cat. of Greek Vases in the Museum in Toronto*, No. 153; for type, Payne, *Necrocorinthia*, p. 283, fig. 121, No. 373, B, No. 376. For a similar vase, see *Corpus Vasorum Antiquorum*, The Robinson Collection, pl. XIV, 6, where parallels are cited.

**Lekythos.** Plate XXXIX, fig. 4.

Height .092 m., maximum circumference .121 m.

Fine tan-colored clay as a base. The body is slender and cylindrical. There is a reserved band over the low, black foot; the neck is long, the mouth spreading, the lip flat; a thick, vertical handle, black above, reserved below, is attached to the neck and shoulder; a black tongue-pattern is on the neck. The body of the vase is decorated with a black, reticulated pattern between black bands.

Greek ware of the Fourth or Third Century B.C.

*Cf.* Robinson, Harcum and Iliffe, *Greek Vases in the Museum in Toronto*, No. 515; and, for squat Lekythos of a very rude type, see Robinson, *Excavations at Olynthus*, Part V, pls. 146-147.



**Aryballos.** Plate XXXIX, fig. 5.

Dimensions about the same as the vase shown in fig. 2, except that the body is nearly round. The design is nearly obliterated. It is a conventionalized lotus design. Late Corinthian, Fifth Century B.C.

For type, *cf.* Payne, *op. cit.*, p. 287, fig. 123, p. 320, No. 1263; Robinson, Excavations at Olynthus, Part V, pl. 443; Corpus Vasorum Antiquorum, Michigan, pl. XI, 9.

**Squat Lekythos.** Plate XXXIX, fig. 6.

Height .065 m., maximum circumference .072 m.

Black glazed vase with metallic lustre. Low foot with narrow, reserved, intersection band. Squat, flat, ribbed body. The loop handle is vertically attached from the shoulder to base of the neck. Trumpet-shaped mouth. Incised vertical lines make ten divisions of the body; each incised line is forked at the base. Probably Attic of the Fourth Century B.C.

Compare for type, Robinson, Harcum and Iliffe, Greek Vases, in Toronto, No. 548.

**Red-figured Kotyle or Owl Skyphos.** Plate XXXIX, fig. 7.

Height .075 m., diameter .097 m.

The cup is covered with a lustrous, black glaze, except the design which is light red, the color of the clay. Shape same as in object figured in British Museum, Cat. of Greek Vases, III, p. 14, fig. 8. On both obverse and reverse there is an owl between olive leaves. There are black dots on the head of the owl and from its neck to its feet.

Attic, First Half of the Fifth Century B.C.

Cecil H. Smith, Brit. Mus. Cat., III, p. 14, says: "This design is familiar on the coins of Athens as an official Athenian symbol, but it is difficult to explain its occurrence on these vases unless on the theory that they have been made for some special or religious occasion. See Robinson, Harcum and Iliffe, Catalogue of the Greek Vases in the Museum in Toronto, Vol. I, p. 183, Nos. 373-375, where many parallels are given. Dinsmoor, William Bell, American Journal of Archaeology, Vol. XXXVIII, 1934, pp. 419-420, "would date some of these owl vases as early as 490 B. C." *Cf.* Baur, Paul V. C., The Rebecca Darlington Stoddard Collection of Greek and Italian Vases, Yale University, figs. 90, 161, 319, 337, 338. Baur thinks the owl may be apotropaic.

The owl, the sacred bird of Athena, and the olive, her gift to the city of Athens,

were placed on the earliest Attic coins. These silver coins retained their primitive appearance through all later stages of Greek Art.

C. F. Seltman, "Athens, Its History and Coinage Before the Persian Invasion," has shown that the owl on the coins, together with the head of Athena, is the most important index of the development of coinage of the Peisistratids. In all these coins the head of the owl is in front view and the body in side view. The owl, figured on the cups, became the trade-mark of Athens; for these cups were exported to all parts of the Greek world.

**Squat Lekythos.** Plate XXXIX, fig. 8.

Height .095 m., maximum circumference .075 m.

Glossy, black glaze, except reserved band at the base. Globous body flattened at top and base. Bell-shaped mouth. Vertical, looped handle. Late Attic, Fourth Century B.C.

*Cf.* Mary A. B. Herford, *A Handbook of Greek Vase Painting*, p. 102, pl. 11d; Robinson, *Excavations at Olynthus*, Part V, No. 469.

**Lekythos.** Plate XL, fig. 1.

Height .093 m., maximum circumference .12 m.

Black on a buff clay ground. A low, reserved foot, black above, supports a reserved pedestal on which rests the body of the vase, which is encircled by three black bands. The body is marked by incised lines, filled with white paint, in a reticulated pattern. There are up-pointing rays on the lower part of the neck. The vertical handle, reserved below, black above, rises from the shoulder and curves down to the base of the neck, which is black above. The mouth, in the shape of an inverted bell, is black with a flaring, black lip. The vase is similar to that shown in fig. 4, plate XXXIX. For type, see Robinson, *Greek Vases in Toronto*, No. 515.

Attic of Fourth or Third Century B.C.

**Red-figured Bell Krater with cover.** Plate XL, fig. 2.

Height to top of cover, .146 m., diameter of mouth .137 m.

Decorations; pale red and white on black ground; light gray clay. Small, low foot, body ovoid-cylindrical, tapering sharply at the base; wide, flaring lip, tongue-pattern below lip, except over the handles, which are curved upward. On the cover there is a half-spool handle; rude shell-patterns enclose two womens' heads, with hair curling in front and a knot projecting from the hair-band in the back. On the

body of the vase, between the handles, on both obverse and reverse, there is a head of a woman in profile, facing the left, between vertical tendrils. The head-band, necklace and decorations are white. Rather rude work.

Apulian, Fourth Century B.C.

*Cf.* Walters, *Anc. Pottery*, Vol. I, p. 487.

**Ænochoe.** Plate XL, fig. 3.

Height .25 m., maximum circumference .316 m.

White, red and yellow on black ground.

Foot, black below; a concave, reserved band above; the base of the vase is decorated with an astragal pattern between narrow yellow bands; the globular body is covered with a diamond pattern (lattice), made by incised lines filled with white paint; there are two narrow yellow bands on the shoulder; on the neck is an elongated yellow-and-white leaf pattern pointing upward; above is a yellow band. Trefoil mouth, a little broken. A round handle rises obliquely from the shoulder and projects over the mouth in the form of a snake's head.

Probably "Gnathia" Ware, Third Century B. C.

*Cf.* Corp. Vas. Antiq. Gr. Brit., Brit. Mus., Fasc. 1, IV. D.c, Gnathia Vases, Pl. 5, 1, and Pl. 7, 5.

**Lekythos.** Plate XL, fig. 4.

Height .165 m., maximum circumference .172 m.

Glossy, black glaze; design white and yellow; no ribbing on the body of the vase. There is a concave, reserved band over the narrow, black foot. The slightly swelling body rises to a slender neck, which expands to a bell-shaped lip. A small, vertical handle extends from the shoulder to the top of the neck. On the lower part of the neck rise short, white rays. On the shoulder there are two yellow bands, next a herring-bone pattern, painted yellow, then two yellow bands. About the body, four white, five-fingered festoons hang from a loose cord.

Gnathia Ware, Second Half of Third Century B.C.

*Cf.* Corp. Vas. Antiq., Br. Mus., IV, D.C., Plate I, II; see Note Pl. VI, 2; Walters, *Hist. of Ancient Pottery*, Vol. I, p. 487 f.

**Guttus**, a variation of the Askos form. Plate XL, fig. 5.

Height .077 m., to top of the spout .123 m.

The whole surface of the vase is covered with a glossy, black glaze, except a narrow, reserved band above the foot.

From the flattened, swelling body rises a high, nearly vertical, spout, with



overhanging lip and a loop-ring handle. On the side between the handle and the spout there are four double-incised lines; the rest of the body is covered with incised lines. On the top of the vase in a medallion there is a female head in bas-relief, perhaps of Medusa; her hair falls in tresses on each side. The face is oval, the mouth nearly obliterated.

Campanian, Third or Second Century B.C.

*Cf.* Walters, *Hist. Gr. Pottery*, Vol. I, pp. 211, 503; *Brit. Mus. Cat. of Greek Vases*, IV, G 37 f.; Baur, *op. cit.*, p. 210, fig. 262.

#### One-handled Jug. Plate XL, fig. 6.

Height .073 m., maximum circumference .12 m.

Small, black-glazed jug. Low foot, cylindrical body, ring handle, from middle of body to base of the lip. Perhaps imitation of metal ware.

*Cf.* Robinson, *op. cit.*, *Greek Vases in Toronto*, No. 569.

#### Guttus with cover. Plate XL, fig. 7.

Height to top of handle .038 m., maximum circumference .29 m.

The vase was covered with a lustrous, black glaze, now dingy. Molded, ribbed body, vertical loop handle at side, spout in front in form of a lion's head. There is a round cover with knob handle and flanges. When the cover is turned it keeps its place, as on a modern tea-pot. Probably it was used as a lamp-filler.

There is some reason for thinking that the vase may be "true Greek and Attic, Fourth Century or later."

Campanian, Second Century B.C.

*Cf.* Robinson, *Harcum and Iliffe, Cat. of Gr. Vases in the Museum in Toronto*, Vol. I, p. 198, No. 555, and the bibliography given there.

*Cf.* Walters, *Hist. Anc. Pottery*, Vol. I, Pl. XLVIII; but this form has a low, flowing spout.

Horace, *Sat. I*, 116-118 speaks of his simple dinner service:

Cena ministratur puris tribus, et lapis albus

Pocula cum cyatho duo sustinet; adstat echinus

Vilis, cum patera guttus, Campania supplex.

#### Epichysis or Pelike. Plate XL, fig. 8.

Height to top of handle .177 m., maximum circumference at projecting rim .365 m.

Reddish-buff clay, partly covered with lustrous brown. Decoration in opaque

white, yellow and red. On the shoulder are palmettes and spirals. On the concave, pyxis-shaped body is a very stylized laurel-and-dot pattern. On the projecting rim are black rays. The vase has a long neck, trough mouth, and a high angular handle. In front, below the neck, there is the rude head of a woman with red hair and white ornaments.

Apulian, Third Century B.C.

This type closely resembles in shape a vase thus described in Walters, *Hist. Anc. Pottery*, Vol. I, p. 179, fig. 47: "a curious form found only in Apulia, and belonging to the extreme decadence of vase-painting, which has a flat, cylindrical body like a round toilet box with moulded edges. It is surmounted by a long, narrow, beak-like, semicylindrical mouth; and the whole effect is awkward and inartistic."

Apulia, Third Century B.C.

*Cf.* Robinson, *Greek Vases in Toronto*, No. 524 f.; Baur, Paul V. C., *Catalogue of the Rebecca Darlington Stoddard Collection of Greek and Italian Vases*, Yale University, p. 172, 283.

**Skyphos.** Plate XL, fig. 9.

Height .05 m., diameter .15 m.

The cup is painted with a black glaze outside and inside. It has a small, low foot and one thick handle, horizontally attached. On one side is the figure of a nude boy, running toward the left, a harp in his left hand, his right hand extended as if to meet a victor. The figure has been repainted in modern times, but the cup is ancient. The cup is a common type.

Attic, Fourth Century B.C.

*Cf.* Robinson, *Excavations at Olynthus*, Part V, Plate 154, fig. 571.

**Red-figured Oenochoe.** Plate XL, fig. 10.

Height .279 m., maximum circumference .332 m.

Decoration, white and yellow.

The ovoid body is set on a short pedestal which spreads out in a low foot. The pedestal, foot and base of the vase have reserved bands. There is a wave pattern to right on the narrow, slanting shoulder, and a high, slender neck with two horizontal yellow bands, below which yellow and white rays descend. The throat expands into a trefoil-mouth. The broad, ribbed handle rises vertically from the shoulder and descends in a loop to the back of the mouth.

Scene: the head of a woman in profile, wearing an elaborate cap; her hair is fastened behind in a knot. Necklace, earrings, diadem and head-ornaments are

white and yellow. In front of the woman's head there is a pair of figures, each composed of three white dots. On the back of the vase there is a palmette pattern; on each side a scroll pattern. The shape of the vase is not graceful. The outline of the face is good.

Apulia, late Fourth Century B.C.

**Red-figured Pelike.** Plate XLI, figs. 1a, 1b.

Height .336 m., maximum circumference .677 m.

The vase is covered with a dull, black glaze, except the decorative parts which are pale red, the color of the clay. Graceful, ovoid body, low cylindrical foot, lipped at the top, a narrow, reserved band at the junction of the foot and the rounded base. A meander and dotted-cross pattern encircles the vase. Ribbed handles rise almost vertically from the shoulders and support the wide, overhanging, flat, cylindrical lip. Below each handle there is a palmette between tendrils.

Obverse: fig. 1a, a woman wearing a chiton and an elaborate head-dress is moving to the right. Her hair is tied in a knot by ribbons which stream behind. She holds suspended in her right hand a wreath, the berries of which consist of raised, yellow dots. With her left hand, she offers a large dish to a nude youth seated on a rock. He is crowned with a fillet which streams behind. He holds a large cluster of grapes carelessly suspended in his left hand, and in his extended right hand a mirror.

Above on the left there is a tablet, or possibly a window. Above on the right there is a rosette above a looped fillet. On the neck there are four rosettes between reserved bands, and two white dots between each pair of rosettes. The ground below the youth's feet is indicated by dots.

Reverse: fig. 1b, two standing youths, epheboi, face each other. The youth on the left is clothed in a chiton and a himation which is wound about his body and thrown over his left shoulder. He rests his extended right hand on a stout staff on which he leans slightly. He appears to be conversing with a youth who stands before him, enveloped, even his arms, in a mantle. The youths wear garlands; their mantles have a narrow border, and they wear shoes. On the neck of the vase is a band of laurel to the left, between reserved bands. Above the youths, there is "a tablet bound with cords wrapped about it several times."

Epheboi are common on Greek vases of this period, especially on Apulian vases.

Apulian, Fourth Century B.C.

Cf. Robinson, Harcum and Iliffe, *Greek Vases in Toronto*, Nos. 394 and 413; Corp. Vas. Antiq., Lecce, Museo Provinciale, Fasc. IV; Brit. Mus. Cat., *op. cit.*, IV, F., 312, 313, 318, 319, 321-330.



**Kylix.** Plate XLI, fig. 2.

Height .05 m., diameter .174 m.

Glossy black glaze, design on unglazed parts dull red. The foot is low and grooved. The stirrup-shaped handles curve upward. In the interior, within a reserved circle, there is a dull, red field, and on it are stamped four palmettes, or buds on stems.

Attic, Fourth Century B.C.

*Cf.* Baur, *Cat. of Stoddard Collection of Greek and Italian Vases in Yale University*, 162, fig. 38; Hans Schaal, *Griechische Vasen aus Frankfurt Samlungen*, Tafel 19 c, and on Tafel 58 h, a black pinax, with four buds on stems.

Many such stamped plates have been found recently. "Some are of the best period of the Fifth Century B.C." *Cf.* Robinson, *Excavations at Olynthus*, Part V, Plates 154-159.

See also black-glaze stamp ware from the Agora in Athens, Homer A. Thompson, *Hesperia*, III, Number 4, 1934, pp. 429 ff.

**Pinax or Plate.** Plate XLI, fig. 3.

Height .05 m., diameter .223 m.

Exterior: A low foot, a reserved band above the foot and on the border.

Interior: On the rim there is a border of black bars; next a pattern of white conventional laurel leaves to left; then an upright wave-pattern to the left between two reserved bands. In the medallion there is the head of a female to the left; her black hair curls down over her ears, from which hang large, white earrings. She wears a double necklace and an open, striped cap, tied in the back with a white ribbon, and decorated in the net-work with six white dots in triplets. In front of the net-work there is a white head-band, on which are nine diagonal bars, dividing into two bands which encircle the base of the head. Below there is a cluster of white spirals. In the field in front there is a pair of three white dots, and a white flower on a stem. The drawing though conventional is pleasing.

Apulian, Fourth Century B.C.

*Cf.* Baur, *Cat. of the Stoddard Collection*, p. 165, 268, fig. 68; Robinson, Harcum and Iliffe, *Cat. of Greek Vases in Toronto*, No. 461.

## ETRUSCAN ASH URNS

**"Canopic" Urn.** Plate XLII, fig. 1.

Height .455 m., maximum circumference .645 m.

The urn is made of red, unglazed terra-cotta, and is probably hand made.

There are white particles on the head and neck; the body is high, ovoid, the foot low and sloping, the handles horizontally attached, inclining upward. An archaic head of a man forms the lid of the jar. It has a low forehead, close-fitting wig, with small shell-curls at sides and in front, bulging eyes set too high under strongly-marked eye-brows; the nose is ugly and flaring, the mouth a mere slit, with compressed lips, the ears are badly formed, the chin is prominent. The metal chain hanging around the shoulders may belong to this vase. Although the head seems an ugly caricature, it is strongly realistic and is evidently meant for a portrait of the person whose ashes were deposited in the jar. Chiusi, Sixth Century B.C., or earlier.

Bibliography of Canopic urns in general: Montelius, *La Civilization Préclassique en Italie*, Stockholm, 1904-1910, 3 vols., plates, 2 vols., text p. 972 ff., plates 219-223; 226; Bianchi-Bandinelli, *Dedolo*, VI, 1925, p. 8 ff.; Giglioli, *Studi Etruschi*, III, 1929, p. 474 f.

The above references were given to me by Dr. D. M. Robinson. See also Walters, H. B., *History of Ancient Pottery*, Vol. II, p. 304; Dennis, George, *Cities and Cemeteries of Etruria*, ed. 3, 2 vols.; Martha, Jules, *L'Art Étrusque*, pp. 330-340; Ducati, Pericle, *Storia dell' Arts Etrusca*, 2 vols., Florence, 1927, Vol. II, Tav. 70, 71. Walters, H. B., *Cat. of Vases in the Brit. Mus.*, Vol. I, Part II, p. 263, fig. 386 = H 245, fig. 387 = H 246.

#### CHIUSI AND THE ORIGIN OF THE ETRUSCANS.

The Etruscan city Camars, probably on the site of Chiusi (Latin Clusium), was settled by Villanovans and perhaps by other Italic tribes centuries before the Etruscans got a permanent foothold in that region. The Etruscans emigrated to Italy, probably from Asia Minor; Herodotus (I, 94) says from Lydia about 850 B.C. They came by sea in small numbers and in repeated incursions. They were not Indo-Europeans, as we know from the evidence of their language, customs, and religious ideas. They were skilled in metal working, in agriculture and in engineering, and were far in advance of the Villanovans and other Italic peoples among whom they settled and whom they subdued. They became the overlords of these rude Italic tribes, who possessed in primitive form those sturdy characteristics which are prominently seen in the Roman people, especially during the period of the early Republic. The more the Etruscans are studied, the greater seems the debt owed them by their Roman conquerors.

A different opinion as to the origin of the Etruscans is held by some scholars, especially by the eminent archæologist F. Messerschmidt. In a recent book, re-



viewed by Dr. G. M. A. Hanfmann (*Amer. Journ. Arch.*, 1936, Vol. XL, No. 3, p. 394 f.), Messerschmidt effectually demolishes the arguments for an oriental origin but in the opinion of the reviewer, "fails to demonstrate the insuperable difficulties of the autochthonic theory."

This theory is stated by Professor Hugh Last, in *The Cambridge Ancient History*, Vol. VII, p. 379 *et. seq.*, who believes that the Etruscans did not come by sea, but that they were of native Italic stock, being derived from a neolithic people and from the Villanovans. Living in a fertile region, rich in mines of copper and iron, they gradually took the lead over the more backward tribes and became the ruling class of the native cities of northern and central Italy. By commerce and intercourse with the East they became wealthy and made progress in the arts.

The origin of the Etruscans is still an unsolved problem. Further investigation of their alphabet and the discovery of new alphabetic forms of tribes that dwelt in Asia Minor may throw light on the origin of the Etruscans.

A brief note on Chiusi (Latin Clusium), a town of considerable interest to students of Roman history and Roman literature, may be in place here.

The legends about Lars Porsenna, king of Clusium, which were put into stirring verse by Macaulay in his "Lays of Ancient Rome," are now being investigated by serious students of history.

Chiusi is situated at a considerable distance from the sea, and is about one hundred miles from Rome. It had numerous contacts with Rome, not all of them unfriendly. Its people were very conservative, adhering to the old Italic customs indigenous in that part of the peninsula. Its early inhabitants were skillful workers in bronze long before the arrival of the Etruscans. The practice of incineration and of depositing the ashes of the dead in sepulchral urns was long retained by the people of Clusium, when other Etruscan cities practiced inhumation. The city carried on a large manufacture and trade in cinerary urns, of which many hundreds are to be found in Italian museums.

Of the many books and discussions treating of Clusium (Chiusi) I will cite a few:

Dennis, George, *Cities and Cemeteries of Etruria*, Vol. II, p. 290, London, 1887; Cameron, Mary Lovett, *Old Etruria and Modern Tuscany*, London, 1909; Taylor, Lily Ross, *Local Cults in Etruria*, Vol. 11, *American Academy in Rome*, 1923, pp. 175-180; Saunders, Catherine, *Vergil's Primitive Italy*, pp. 64-67, Oxford, 1930; for early and later sculptures, sarcophagi, and urns, from Chiusi, *see* *Catalogue of Sculpture in the Department of Greek and Roman Antiquities of the British Museum*, Vol. I, Part II, *Etruscan Sculpture*, D 8-19 and D 35-51, by F. N. Pryce, London, 1931.



## ETRUSCAN PORTRAIT SCULPTURE

This topic was suggested by the canopic urn in our collection, which has been described above and is shown on plate XLII, figure 1. The examples cited below are well known and of course could be greatly multiplied. Frequent references to the volumes of the Cambridge Ancient History, which are easily accessible, are given in this account.

The advance from the rude, primitive attempts at human portraiture to perfected portrait sculpture may be briefly stated.

First, about 700 B.C., a death-mask of clay or bronze began to be attached to the cinerary urn. This was an indigenous custom in northern Etruria, and it was not derived from the Egyptians or Mycenæans as some writers have thought.

The Etruscans believed that the human personality was perpetuated, if its mundane likeness was preserved for posterity. The wax masks and portrait busts of the deceased, set up in the atria of Roman houses, were survivals of this idea.

Hans Muhlestein, *Die Kunst der Etrusker*, p. 227, pl. 147, describes two bronze death-masks in the Museo Communeale, Chiusi, and also a bronze death-mask and a clay mask (pl. 148) from Chiusi, in the Florence Archæological Museum.

Two terracotta heads from Veii, now in the Museo Gregoriano, Vatican, are described in the *Camb. Anc. Hist.*, Vol. IX, p. 808, and Volume of Plates IV (a). They are excellent life-like portrait heads.

Second, Canopic urns, similar to the urn in the Carnegie Museum previously described, were followed by canopics with heads of terracotta, and with rudely modelled breasts and arms instead of handles. These urns date from about 750-650 B.C.

As examples of two early Etruscan urns in the form of the human figure, see (1) a sepulchral urn from Chianciano, near Chiusi, in the form of a life size standing man, and (2) an urn in the form of a seated man, also life size, from Chiusi. *Cf.* *Cat. of Sculpture in the Brit. Mus.*, Etruscan, Vol. I, Part II, pp. 162-164, fig. 7=D8, and Pl. II, and fig. 8=D9; (3) a still earlier work, a statue of a woman of half life size, from the Polledrara Tomb, Vulci, *Brit. Mus. Cat. (op. cit.)*, pp. 155-157, fig. 1=D1, and Pl. I.

The Apollo of Veii will be mentioned later.

From the canopic urn also was developed the ash chest, on the lid of which sat or reclined an image of the deceased. It need not be supposed that there was commonly much effort made by the artisan or artist to reproduce an exact portrait

of the deceased. The chests were manufactured in immense numbers at Chiusi, Volterra, and elsewhere. A buyer came and chose what seemed appropriate. The reliefs were painted in various colors, many of them most gaudily, and the tombs, in which the sarcophagi have been found, were with their brilliantly frescoed walls by no means all gloomy and terrible. Many of the wall-paintings in the tombs depict the happy and sensuous life of the Etruscans.

In addition to the many hundred chests and larger sarcophagi with reliefs and inscriptions that have been described, there remain many more still undescribed. They give us glimpses of the life and beliefs of this mysterious people from whom the Romans derived so much of their civilization.

For a useful introduction to Etruscan funerary urns and sarcophagi, consult F. M. Pryce, *Brit. Mus. Cat. of Sculpture*, Vol. I, Part II, pp. 148-155, London, 1931.

Many of the recumbent figures on the covers of the sarcophagi are fine specimens of Etruscan sculpture. Three examples may be mentioned here:

(1) An elderly corpulent man, "Obesus Etruscus," reclines on the lid of an urn in the Florence Museum. *Cf.* R. West, *Römische Porträt-Plastic*, p. 18, pl. IV, 9; *Camb. Anc. Hist.*, Vol. IX, p. 810, and Plates IV, p. 40a.

(2) There are the reclining figures of an old man and his old wife, from Volterra, not at all beautiful, but a masterpiece of realism. *Cf.* Ducati, *op. cit.*, p. 548, pl. 270, fig. 656; A. Heckler, *Greek and Roman Portraits*, p. 25; *Camb. Anc. Hist.*, IX, p. 811, Plates IV, p. 40c.

Compare with this successful, technical treatment of an old couple, the relief on the *stele* of C. Septimius, from Vulci, perhaps belonging to the late Republican or early Augustan period, now in the Ny Carlsberg Museum. It is said to be "one of the best examples of a portrait where all the characteristics of a death-mask with the exception of the eyes are observed" *Cf.* *Camb. Anc. Hist.*, IX, p. 814, and Plates IV, pp. 50a.

(3) A work not so well known is the splendidly executed figure of a man reclining on the lid of a Greco-Roman sarcophagus found near Chiusi, of about the year 350 B.C. It is now in a private collection. It is described by F. N. Pryce, in the *Burlington Magazine*, 1926, Vol. 48, pp. 243-251.

Mr. Pryce's description of this recumbent figure in his fine article is so appropriate that at this point I quote a portion of it: "In striking contrast to the Hellenic grace of the relief on the chest is the stark realism of the figure on the lid. The old man with wrinkled face, thinned hair and flabby body is portrayed with miraculous accuracy. Here is a portrait of the native Etruscan school untouched by Greek idealism and showing the fidelity to nature which Etruria handed down to Rome."



For the finest example of Etruscan plastic art we must go back to about the year 500 B.C. to the grand terracotta figure of the Apollo of Veii, now in the Villa Giulia, Rome, representing the relentless deity of the Etruscan pantheon. It was made under Ionian-Greek influence, but it is Italic in character. There is reason to believe that the maker of the Apollo was Vulca, the Etruscan sculptor who made the statue of Jupiter in the Capitoline temple at Rome.

Bibliography: Ducati, *op. cit.*, p. 230, 252, Tav. 99, 100, figs. 266, 267; G. Kaschnitz-Weinberg, Studien zur Etruskischen und Frürrömischen Porträtkunst, in Röm. Mitt. XLI, p. 133f, 1926; G. Q. Giglioli, Etruskische Terrakottafiguren aus Veii, Antike Denkmäler, III, Berlin, 1926; D. Randall-MacIver, The Etruscans, 1927; Camb. Anc. Hist., Vol. IV, p. 424, Plates Vol. I, p. 334, and Vol. IX, p. 813, Plates IV, p. 48d; F. Poulsen, Das Helbig Museum, Copenhagen, 1927; G. Buonamici-A. Neppi Modona, A Guide to Etruscan Antiquities, Florence, 1928; M. A. Johnstone, Etruria Past and Present, London, 1930.

I will close this condensed sketch of Etruscan portrait sculpture by a reference to the famous bronze statue, L'Arringatore, the "Orator," in the Florence Museum discovered near Lake Trasimene. It belongs within the years 218-190 B.C. The Etruscan inscription on the edge of the robe gives the name of the personage as that of Aules Metelis (Latin, Aulus Metilius). The head shows Italo-Etruscan derivation, but the character of the figure as a whole is definitely Roman. It is a transition work. To quote Mrs. Eugénie Strong, Art in Ancient Rome, Vol. I, p. 70: "It is an example of a portrait midway between the Etruscan manner and the newer Roman style influenced by Greek models." Cf. Ducati, *op. cit.*, p. 546, Tav. 267, fig. 651; Camb. Anc. Hist., Vol. IX, p. 813, and Plates IV, p. 48, (d).

Whatever was the influence of Greek sculpture on Roman portrait sculpture the genesis of the art can be traced to the Etruscans.

Of course the Etruscans, so lacking in imagination and idealism, did not create really great works after the manner of the Greeks in the arts of painting and sculpture. In the words of Mr. Stanley Casson, Camb. Anc. Hist., Vol. IV, p. 432, "The artist as a general rule failed to understand the underlying methods of balance, proportion and construction which were the essential qualities of his Greek prototypes. In consequence his work was deprived of the vigor of true artistic creation; it had no natural inspiration."

#### Ash Urn with Lid. Plate XLII, fig. 2.

Height .368 m., to the top of the cover .622 m.

Length: .54 m., width .228 m. Alabaster. On each end of the chest is a large rosette in relief, perhaps symbolic of the flowers of the resurrection.



On the lid reclines the figure of a fat, middle-aged man, the body somewhat shortened. His left arm rests on two tasselled pillows. He is obese and sensual looking. His short hair is combed over his forehead. He wears a fillet and a garland and a robe draped over his left shoulder and covering his legs and feet. In his extended right hand he holds a *phiale mesomphalos*, resting on his knees. On the third finger of his left hand is a ring with a flat bezel.

The face is well modelled except the ears. The chin is prominent. The hand is large and the fingers are very long.

The figure is that of an Etruscan noble whose ashes were deposited in the chest underneath.

The scene on the chest is in high relief. On a slightly extended base, decorated with a conventional leaf-design, two warriors at the point of death face each other on their knees. They wear Phrygian caps, and cheek-pieces, also corselets, shoulder straps, and embossed belts; below the metal flaps on the corselets, the edge of the chiton appears. Eteokles on the left wears a chlamys, fastened in front with a brooch. He leans on his upright shield, held close to his side, and grasps his heavy sword at an angle, the point touching his thigh.

The warrior on the right, Polyneikes, leans back weakly on his shield, holding his sword in a spent manner across his thigh, his left arm hangs down helplessly. The Theban brothers are about to expire from each other's sword thrusts.

The modelling of the figures is good and shows decided Hellenic influence. Physical suffering appears on the faces, especially in the mouths, and in the drooping heads. The balance of the relief is well preserved, but monotony is avoided by individual differences in the attitudes, and in details in the representation of the warriors.

In the centre of the scene sits a female death-angel, Lasa, with winged helmet, long hair flowing down her neck at each side, and a band about her shoulders, fastened cross-wise between her breasts by a brooch. She wears a chiton, held at the waist by an embossed girdle, and high boots. Her arms, breasts, and legs are bare.

On each of her large, outstretched wings is an eye, perhaps a symbol of speed or of unerring foresight. The face of the Fury or Lasa has a fixed, relentless, stony stare. Otherwise she is not physically repulsive. In her right hand she holds up a heavy bar, her left hand rests on the stone on which she sits.

Volterra, Third or Second Century B.C.

*Cf.* Brunn-Körte, *op. cit.*, II, pp. 41 ff., Pl. XIV, 3, XIII, 1, taf. 188, 11, p. 263, Pl. XVII, 1; in the Chiusi Museum there are numerous examples, also in the Volterra Museum; and in the Archæological Museum, Florence; *Cf.*, Inghirami, I.

tav. 92, 93, VI, tav. V, 2; Dennis, *op. cit.*, II, p. 364; F. N. Pryce, *Cat. of Sculp. in the Brit. Mus.*, Vol. I, Part II, Fig. 61 = D 40-1, pp. 205-206.

This Theban story may be the foundation of the Roman-Etruscan saga of Brutus and Aruns. Cf. F. Poulsen, *Cat. of the Helbig Museum der Ny Carlsberg, Glyptoteek H. 297*. Cf. Dion. Halic., V. 15; Livy, II, 6, 79; Cicero, *Tusc. Disput.*, IV, 50: *Ut numque cominus ictu cecidisse contrario*.

These literary references are taken from Poulsen, *Helbig Museum, H. 297*, p. 144.

#### Ash Urn. Plate XLII, fig. 3.

Height .26 m., length .444 m., width .215 m.

Terracotta. The relief is set in a panel. On each side a pseudo-ionic pilaster is painted; above is an ovolo molding. The inscription along the upper border of the chest, painted in red letters, is illegible.

The scene represents a combat between two warriors, Eteokles and Polyneikes, a favorite relief on these urns.

Eteokles advances to the right, bends forward and stabs in the throat Polyneikes, who has fallen on his right knee and is stabbing his opponent in the belly with an upward thrust. With his left hand Eteokles holds back the shield on the other's left arm. His own shield, on which Polyneikes leans, can be seen in front of his left knee. Each warrior wears a crested helmet, cuirass and short chiton. Polyneikes' helmet, however, now lies on the ground below Eteokles. The latter wears a chlamys.

The bull-like head of Polyneikes in the Plate is due, of course, to the wearing away of the clay relief.

At either end a winged Death-angel, Lasa, is moving away and looking back and extending her inner arm over the nearer warrior. They have small wings and wear short-girt chitons, with cross-bands fastened with brooches, and high boots turned over at the top. Each holds a lighted torch in the outer hand. The faces of all the figures are much worn. The paint on the relief is gone. Probably from Chiusi, Third Century B.C.

Cf. *Cat. of Terracottas of the British Museum*, D. 788, 792, 799, 800; Brunn-Körte, I. *Rilievi dell'urne Etrusche*, Vol. II, p. 32 ff., pl. XI, 2, and pl. 19, fig. I, p. 32 ff.; Brunn-Körte, *op. cit.*, Vol. III, 1916, p. 67 f., fig. 2, pl. LVII, 7; *Arch. Anz.*, XLIII, 1928, p. 388 ff., fig. 102; *Bull. of the Fogg Museum*, III, 1, 1933, p. 16, fig. 6; one specimen is in the Johns Hopkins University Collection. Cf. Dennis, *op. cit.*, II, p. 165; *Cat. Brit. Mus.*, IV, G 104, a Megarian Bowl on which are scenes from the *Phoenissæ* of Euripides.



For a series of urns depicting the story of this combat, *cf.* Brunn-Körte, *op. cit.*, Vol. II, Part I, Ch. IX, pp. 27-56, and plates IX-XIX.

**Ash Urn.** Plate XLII, fig. 4.

Height .209 m., length .304 m., width .185 m.

Terracotta. In a panel is a relief representing a parting scene. In the centre is an arched door-way, which may be the gate of Hades or the door of the soul. On the doors, below a cross, are two lions' heads, each holding in its mouth a metal ring. The rings are fastened together to close the entrance. Before the doors stand two figures, facing front, a man and a woman, clasping each other's right hand. They gaze intently at each other. Each wears a chiton and a himation twisted about the left shoulder, leaving the right arm bare. The man tries to draw back the woman. Her left arm is extended downward to the left.

Behind the man, facing front and to the left, stands a nude, muscular winged Death-angel, Charon. He wears boots and a cap or hood and a lion skin crossed over his chest, and he holds in front in his right hand a heavy hammer which rests on the ground. On the woman's left stands a female Death-angel, Lasa, facing front to the left, wearing a cap, boots rolled down at the top, chiton and a cross-band, fastened by a brooch between the breasts. The demon holds suspended in front in her right hand a heavy, sheathed sword, and her left hand rests on her left thigh. All the faces in the relief are too worn to be clearly distinguished.

At each side an Ionic column with vertical lines painted red supports the architrave on which was painted in black letters an inscription, most of which is now illegible.

Parting scenes on cinerary urns are very common. Some of these were perhaps suggested by the story of Admetus and Alcestis, frequently represented on Greek vases. If this is the case here, the figure at the left may be Herakles and the one to the right Thanatos. The whole work is crude, but the attitudes are most realistic.

Chiusi, Third or Second Century B.C.

*Cf.* Cat. of Terracottas, Brit. Mus., IV, D 796, F 486; Dennis, *op. cit.*, II, frontispiece; Walters, *op. cit.*, II, p. 310.

**Lid of an Ash Urn.** Plate XLIII, fig. 1.

Height .245 m., length .41 m., width .225 m.

Terracotta. The white slip which originally covered the figure is now largely worn off, leaving the brick-red color of the clay.

On the lid a young man reclines at ease in a semi-upright position. He wears



a chiton, and a himation thrown over his left arm and shoulder and covering his legs. His left arm rests on a tasselled pillow; his right hand holds a *phiale mesomphalos* against his right knee which is drawn up; his right foot seems to rest on a pillow. On the third finger of his left hand is a seal ring. The face, except the nose and right eye, is well preserved. Hellenic influence is seen in the head and drapery. There is considerable dignity in the figure.

Chiusi, Third or Second Century B.C.

*Cf.* Cat. of Terracottas, Brit. Mus., IV, D 787, 795.

**Lid of an Ash Urn.** Plate XLIII, fig. 2.

Height .31 m., length .44 m., width .22 m.

Gray terracotta.

On the lid of the urn is the figure of a woman reclining, her left arm resting on a pillow. She gazes upward with a rapt expression. Her hair is parted and waved. She wears a chiton tied at the waist with a ribbon, and a himation, covering her legs, and drawn back with her right hand so as to cover the back of the head, shoulders and left arm. The right knee is drawn up, and the left knee is bent. The right foot seems to rest on a pillow. Much skill is shown in the modelling of the hair, the folds of the garments and the features. Greek influence is apparent in the figure.

Chiusi, Third or Second Century B.C.

For parallels, *cf.* Cat. of Terracottas, Brit. Mus., covers or lids of 791 and 792.

**Ash Urn.** Plate XLIII, fig. 3.

Height .213 m., length .342 m., width .19 m.

Terracotta. Upper left corner is broken off. At each end a decorative column painted red encloses a panel on which is a relief representing a combat. Near the centre a youth in back view and nude, except for a hat and a red sash wound about his waist, strides to the left and with both hands drives a long, heavy plough-share against two warriors, one of whom has fallen on his left knee, while the other, with drawn sword and shield, stands over his fallen comrade to protect him. The fallen man, facing front, under cover of his shield looks back and brandishes his sword in his extended right hand in the vain attempt to defend himself. He wears a helmet, cuirass with a row of flaps, and a short chiton. His comrade behind him wears a crested helmet, and perhaps a chlamys fastened at the neck with a brooch. On the extreme right a warrior facing to the front, covered by his shield, retreats to the right. His right arm holds a sword as he looks back at the combat. The outside of the shields are painted yellow with brown decorations; parts of the relief

show traces of red paint. The features of the warriors are largely obliterated. The bodies are well molded, evidently under Hellenic influence. The relief is in rather a bad condition.

Chiusi, Third or Second Century B.C.

Above the relief there is a retrograde inscription painted in red letters.

For the transcription and interpretation of the inscription on the urn represented on Plate XLIII, figure 3, see page 339.

The subject of the relief has been interpreted as Echetlos fighting at the battle of Marathon. Cf. Pausanias I, 32, 5, and II, pp. 443-444, in Frazer's Edition; B. M. Cat. of Terracottas, D. 796; Dennis, *op. cit.*, Vol. II, p. 166; Roscher, Lexikon I, p. 1212, thinks the scene may refer to Etruscan mythology. Körte interprets the figure with the plough as the hero Tarchon saving the Etruscans from invasion. For Tarchon, cf. Müller-Deecke, II, pp. 283-284. Cf. Munich, Museum f. Antike Klein Kunst, pp. 14 ff.

#### Ash Urn with Lid. Plate XLIII, fig. 4.

Height .203 m., length .29 m., width .13 m.

Gray terracotta, originally covered with a white slip.

On the cover reclines a woman in the sleep of death. She is completely enveloped. Her head and shoulders rest on a high, double cushion. Her hair is in a thick roll.

In a panel the relief represents a death scene. In the center stands a winged female Death-angel, Lasa, to right, facing front. She wears a himation and chiton and perhaps a hat. In her left hand she holds up a large, lighted torch. With her extended right hand she grasps the arm of a woman wearing a long, loose robe and boots, and draws her to the right toward Cerberus who stands with open jaws. Behind the monster stands Charon, facing front, clad in a himation, one end of which is thrown over his left shoulder and wound about his waist. His chest and right arm are bare. He holds in his extended right hand a bowl and in his left hand a small object, perhaps poppy seed. Charon directs the way to a narrow, vaulted portal, closed by double doors, on which rings and hinges are visible, the entrance to the lower world, or perhaps it is the door of the soul. A dentil decoration is back of the figures. Above the relief is a retrograde inscription painted in black letters. For the transcription and interpretation of this inscription, see page 339.

Chiusi, Third Century B.C.

Bibliography: Brunn-Körte, *op. cit.*, p. 68, fig. 13, pl. LVII, 8.

## THE INTERPRETATION OF THE INSCRIPTIONS.

For the interpretations of the inscriptions on the two Ash Urns which are shown on Plate XLIII, figs. 3 and 4, I am indebted to Professor Eva Fiesel of Bryn Mawr College who kindly made them from tracings of the inscriptions which had been taken by Dr. G. M. A. Hanfmann of Harvard University.

Inscription from Ash Urn shown in figure 3, plate XLIII.

**A 7 1nV9t:11:11n1913Y:11A0**

Thana: thetrinei: vetrunisa. . . = "Thana Tetrinia Vetroni (uxor)." The inscription (all four of them) belongs to the general type on urns from Central Etruria, most of them dating from the third or second century B.C. They gave the name of the deceased, eventually the name of the husband, often the name of the mother (prænomen and gentile name). They are not found however in these two inscriptions. Thana (than(i)a) is a well known Etr. prænomen femini generis. Thetrinei is the feminine form of a Masculinum thetrina (gentile name of the father). The same name occurs in Latin Tetrinius? See W. Schulze, *Zur Geschichte Lateinischer Eigennamen*, 125, 242. The name of the husband is expressed by the Suffix -sa, The nominative would be vetruni(e), Latin Vetronius, which is found in Chiusi, C. I. E. 1148. See Schulze, *loc. cit.*, 191. Both are derivations from a name vetru, also recorded in Chiusi, C. I. E. 1902.

Inscription from Ash Urn shown in figure 4, plate XLIII.

**111tV9A):11:11LYA:11A0**

Thana aulia: vl.: carut es = "Thana Aulia, Veli (?) (filia), Caruti (uxor). Aulia, Masculine aule, aulie, is a well known female name, found both as a prænomen and a gentile name (the latter in this inscription). Latin Aulus, Aulia. As to Latin Carutius, which corresponds to Etr. Carute, see Schulze, *loc. cit.*, 146. The abbreviation is to be read al. according to Hanfmann's design. But I would think it more likely that we have to read vl. for velus, a very common abbreviation. Velus is genitive of the masculine prænomen vel.



## EXPLANATION OF PLATE XXXVII

Black-figured Column Krater or Kelebe.

Attic, c. 530-520 B.C., Chiusi.

Obverse: Achilles and Ajax playing.

The reverse side of this Krater is figured on Pl. XXXVIII.









## EXPLANATION OF PLATE XXXVIII

Black-figured Column Krater or Kelebe.

Attic, c. 530-520 B.C., Chiusi.

Reverse: Youths at Exercise.

The obverse side of this Krater is figured on Pl. XXXVII.









## EXPLANATION OF PLATE XXXIX

- FIG. 1a. Black-figured Eye Kylix. Attic, Early Sixth Century B.C. Exterior, Satyrs and Mænads.
- FIG. 1b. Interior of Kylix shown in fig. 1a. A Gorgoneion.
- FIG. 2. Aryballos. Italic Corinthian, perhaps Sixth Century B.C.
- FIG. 3. Alabastron. Etruscan or Italian imitation of a Corinthian alabastron. Early Sixth Century B.C.
- FIG. 4. Lekythos, Greek ware of Fourth or Third Century B.C.
- FIG. 5. Aryballos, late Corinthian, Fifth Century B.C.
- FIG. 6. Squat Lekythos, probably Attic, Fourth Century B.C.
- FIG. 7. Red-figured Kotyle or Owl Skyphos, Attic, first half of Fifth Century B.C.
- FIG. 8. Squat Lekythos, Late Attic, Fourth Century B.C.





1a



1b



2



3



4



5



6



7



8







## EXPLANATION OF PLATE XL

- FIG. 1. Lekythos, Attic, Fourth or Third Century B.C.  
FIG. 2. Red-figured Bell Krater with cover. Apulia, Fourth Century B.C.  
FIG. 3. *Ænochoë*. Probably "Gnathia" Ware, Third Century B.C.  
FIG. 4. Lekythos, Gnathia Ware, Second half of Third Century B.C.  
FIG. 5. Guttus, a variation of the Askos form, Campanian, Third or Second Century B.C.  
FIG. 6. One-handled Jug. Perhaps imitation of metal ware.  
FIG. 7. Guttus with cover. Attic or possibly Campanian under Attic influences. Fourth Century B.C.  
FIG. 8. Epichycis or Pelike. Apulian, Third Century B.C.  
FIG. 9. Skyphos. Attic, Fourth Century B.C.  
FIG. 10. Red-figured *Ænochoë*. Head of a woman in profile. Apulia, late Fourth Century B.C.



1



2



3



4



5



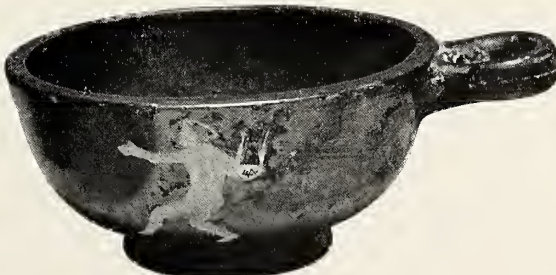
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9



10







## EXPLANATION OF PLATE XLI

- FIG. 1a. Red-figured Pelike. Obverse, woman and seated youth.  
FIG. 1b. Reverse of object shown in fig. 1a, two standing youths.  
Apulian, Fourth Century B.C.  
FIG. 2. Kylix. Black stamped ware. Attic, Fourth Century B.C.  
FIG. 3. Pinax or Plate. Female head in the medallion. Apulian, Fourth Century B.C.



1a Obverse



2



1b Reverse



3







## EXPLANATION OF PLATE XLII

- FIG. 1. "Canopic" Urn. Chiusi, Sixth Century B.C.
- FIG. 2. Ash Urn with Lid: Combat of Eteokles and Polyneikes. Volterra, Third or Second Century B.C.
- FIG. 3. Ash Urn. Combat of Eteokles and Polyneikes. Probably from Chiusi, Third Century B.C.
- FIG. 4. Ash Urn. A parting scene. Chiusi, Third or Second Century B.C.





1



2



3



4







## EXPLANATION OF PLATE XLIII

- FIG. 1. Lid of an Ash Urn: a young man semi-recumbent. Chiusi, Third or Second Century B.C.
- FIG. 2. Lid of an Ash Urn: a young woman semi-recumbent. Chiusi, Third or Second Century B.C.
- FIG. 3. Ash Urn. Combat of Warriors. Chiusi, Third or Second Century B.C. For the transcription and interpretation of the inscription on this chest, see p. 339.
- FIG. 4. Ash Urn with Lid. A death scene. Chiusi, Third Century B.C. For the transcription and interpretation of the inscription on this chest, see p. 339.



1



2



3



4





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